Genome size versus geographic range size in birds

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Why do some species occur in small, restricted areas, while others are distributed globally? Environmental heterogeneity increases with area and so does the number of species. Hence, diverse biotic and abiotic conditions across large ranges may lead to specific adaptations that are often linked to a species’ genome size and chromosome number. Therefore, a positive association between genome size and geographic range is anticipated. Moreover, high cognitive ability in organisms would be favored by natural selection to cope with the dynamic conditions within large geographic ranges. Here, we tested these hypotheses in birds—the most mobile terrestrial vertebrates—and accounted for the effects of various confounding variables, such as body mass, relative brain mass, and geographic latitude. Using phylogenetic generalized least squares and phylogenetic confirmatory path analysis, we demonstrated that range size is positively associated with bird genome size but probably not with chromosome number. Moreover, relative brain mass had no effect on range size, whereas body mass had a possible weak and negative effect, and range size was larger at higher geographic latitudes. However, our models did not fully explain the overall variation in range size. Hence, natural selection may impose larger genomes in birds with larger geographic ranges, although there may be additional explanations for this phenomenon.
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Abstract

Why do some species occur in small, restricted areas, while others are distributed globally? Environmental heterogeneity increases with area and so does the number of species. Hence, diverse biotic and abiotic conditions across large ranges may lead to specific adaptations that are often linked to a species’ genome size and chromosome number. Therefore, a positive association between genome size and geographic range is anticipated. Moreover, high cognitive ability in organisms would be favored by natural selection to cope with the dynamic conditions within large geographic ranges. Here, we tested these hypotheses in birds—the most mobile terrestrial vertebrates—and accounted for the effects of various confounding variables, such as body mass, relative brain mass, and geographic latitude. Using phylogenetic generalized least squares and phylogenetic confirmatory path analysis, we demonstrated that range size is positively associated with bird genome size but probably not with chromosome number. Moreover, relative brain mass had no effect on range size, whereas body mass had a possible weak and negative effect, and range size was larger at higher geographic latitudes. However, our models did not fully explain the overall variation in range size. Hence, natural selection may impose larger genomes in birds with larger geographic ranges, although there may be additional explanations for this phenomenon.
Introduction

There is enormous variation in the sizes of species’ geographic ranges (Gaston 2003). There are several explanations for this, with leading hypotheses invoking traits such as body size (Cambefort 1994; Gaston & Blackburn 2000), dispersal ability (Lester et al., 2007; Laube et al., 2013), and niche breadth (Garcia-Barros & Romo Benito 2010). The increase in geographic range size is consistent with environmental variability (for example, climate), which is considered a major selective evolutionary force (Lee-Yaw & Irwin 2012; Sayol et al., 2016; Liedtke et al., 2018). Therefore, species possess numerous traits for living in dynamic environments (Gaston & Blackburn 2000; Zamudio et al., 2016). These traits have strong heritable components and are thus linked with gene number (Zhang et al., 2014). Hence, genome size could be an important predictor of a species’ range size and could affect other species’ traits subject to natural selection.

The evolution of genome size is multifaceted (Lefèbure et al., 2017). According to the “selection hypothesis”, the variation in genome size has consequences on organismal fitness and may thus be subject to selection (Gregory & Hebert 1999; Petrov 2001). Corroborating this hypothesis, Hou & Lin (2009) found a strong positive association between the log-transformed values of protein-coding gene number and genome size in eukaryotes and non-eukaryotes. In eukaryotes, genome size may be defined as the C-value, which is the amount of DNA per haploid genome and chromosome number. Genome size regulates the cell size associated with polyploidy, possibly leading to instantaneous shifts in the physiological tolerance and trait values (Levin 2002). Alternatively, according to the “junk DNA” hypothesis, the propagation of selfish intragenomic transposons and other mobile genetic elements leads to the accumulation of mutations throughout the genome, yielding a larger genome size (John & Miklos 1988; Bennetzen & Kellogg 1997). Indeed, organisms with larger genomes tend to have longer introns and more transposable elements than organisms with smaller genomes (Lynch & Conery 2003; Charlesworth & Barton 2004).
These two hypotheses are often combined by postulating adaptive functions of this additional DNA, given that DNA abundance, rather than its contents, produces a direct and significant effect on the phenotype (Petrov 2001). For instance, a larger genome size may be an adaptive strategy, because it may directly or indirectly increase the nuclear and cellular volume (Cavalier-Smith 1978) and body size (Gregory 2005), buffer fluctuations in the enzyme concentrations, or protect the coding DNA from mutations (Hsu 1975; Janssen et al., 2018). Likewise, genome size is correlated with cell cycle complexity (Gregory 2002; Yu et al., 2019), basal metabolism (Vinogradov 1997), tissue differentiation, and developmental rate (Sessions & Larson 1987; Xia 1995; Wyngaard et al., 2005). Arnqvist et al., (2015) showed that females with larger genomes laid more eggs and males with larger genomes fertilized more eggs in beetles.

The hypothesis regarding genome size versus geographic range size has already been tested in bacteria and plants. Bacteria with larger genomes are more likely to have wider environmental and geographic ranges than those with smaller genomes (Barberán et al., 2014; Choudoir et al., 2017). In contrast, while plant invasiveness is negatively associated with genome size but positively associated with chromosome number (and ploidy level), plant genome size is positively associated with chromosome number (Pandit et al., 2014). However, this hypothesis has not been tested in vertebrates.

In contrast to plants, genome size (C-value) may be weakly but positively correlated with chromosome number in animals (Vinogradov 1988; Elliott & Gregory 2015). Chromosome number plays pivotal roles in speciation, sex determination, and developmental modes (King 1995; Warchałowska-Śliwa et al., 2011; Blackmon et al., 2017; Lucek 2018). Thus, chromosome number may also be positively associated with geographic range size (Guo et al., 2003; Martinez et al., 2017).

Birds are a unique and useful model group to test many evolutionary hypotheses. They have a limited genome size compared to other vertebrates, ranging from 1.15 to 1.62 pg of DNA per haploid genome (Andrews et al., 2009). However, there is substantial variation in avian karyotypes; as such, the chromosomes are further divided into macro- and microchromosomes (Kretschmer et al., 2018; Degrandi et al., 2020). Avian genomic diversity covaries with adaptations to different life strategies and convergent evolution of traits (Zhang et al., 2014). Most birds possess the ability to fly; they are thus not as constrained by physical barriers, as are
other organisms. Range size in birds is therefore often correlated with their dispersal ability (Böhning-Gaese et al., 2006; Laube et al., 2013). However, avian flight required massive changes (for light weight and increased energy efficiency) of all aspects, including the size of the genome (Zhang et al., 2014). In birds amount of DNA gained by transposable element expansion is counteracted by DNA loss from large segmental deletions (Kapusta et al., 2017; Zhang et al., 2014). Nevertheless, bird genome size is positively associated with the nuclear or cellular size and wing loading index, which is an indicator of adaptation for efficient flight (Andrews et al., 2009). Hence, a positive association between genome size and geographic range is anticipated in birds.

The alternative (but not mutually exclusive) hypothesis is that large geographic ranges favor enhanced cognitive skills, enabling survival in dynamic conditions across these ranges. Cognitive skills are linked to a large brain (Reader & Laland 2002; Sol et al., 2005; Emery 2006) and seemingly to habitat generalism (Edmunds et al., 2016; Navarrete et al., 2016). Indeed, bird species exposed to greater environmental variation throughout their geographic range are likely to have larger brains (Sol et al., 2005; Sayol et al., 2016). Therefore, geographic range size may be positively correlated with brain size. In addition, brain size is strongly correlated with body size (Minias & Podlaszczuk 2017). Thus, body size should always be considered a covariate in range size and genome studies, because there is a well-documented paradigm of overall positive association between body size and range size in animals (Gaston & Blackburn 2000; Newsome et al., 2019).

Most bird lineages have diversified within rather restricted regions, and many tropical species are highly reluctant to cross unfamiliar habitats despite being able to fly (Gillies & St. Clair 2010). In terms of their adaptability to a broad range of climates, it is often assumed that birds are constrained by niche conservatism, which appears to be asymmetrical. Ancient tropical groups cannot easily adapt to, or expand into, cold climates; however, groups that have evolved at high latitudes and are cold tolerant are actually thermally flexible and can easily adapt to new climates. They are therefore often the founders of breeding populations (and species proliferation) within the tropics (Smith et al., 2012; Khaliq et al., 2015; Winger et al., 2019). Thus, the range size of birds is expected to be larger at higher latitudes.
To this end, in this study, we tested the hypothesis that genome size, chromosome number, relative brain size, body size and latitude are positively associated with geographic range size in birds. Efficient testing of the causality of such associations on a broad taxonomic scale has proven difficult in the past due to the intercorrelations and phylogenetic non-independence of these biological traits. Thus, we used phylogenetic generalized least squares (PGLS) and phylogenetic confirmatory path analysis (PPA) to control for phylogeny and evolutionary constraints while accounting for the multicollinearity of variables.

Methods

Data collection

Data on bird species’ ranges were collected from BirdLife International (2019) (http://datazone.birdlife.org/species/requestdis). Data were manipulated in QGIS 3 Noosa (QGIS Development Team 2019). To calculate range areas, the Bonne equal-area transformation (ESRI: 54024) was applied. Only extant native ranges were used (Ravilious et al., 2015). Bird phylogenetic trees (Jetz et al., 2012, 2014) based on the constraints described by Hackett et al., (2008) were created in a nexus format online (http://birdtree.org). Sets of 1,000 trees were downloaded for three data subsets (see below).

The method used by Jetz et al., (2012, 2014) allows the inclusion of taxa for which there are no real-time data; this can yield some very problematic results (Hosner et al., 2015; Wang et al., 2017). However, newer avian megaphylogenies are available (Ksepka et al., 2020). The tree created by Ksepka et al., (2020) is based on the reanalysis of the supermatrix described by Burleigh et al., (2015). Ksepka et al., (2020) used constraints from the tree reported by Jarvis et al., (2014), which reflects analyses of approximately 40 Mbp of aligned data and includes over 10,000 loci. The tree created by Ksepka et al., (2020) includes fewer species than that created by Jetz et al., (2012, 2014); however, we used a subset of species present in both to assess whether the results of statistical analyses differ between the two trees.

Data on species genome size were compiled from the Animal Genome Size Database (http://www.genomesize.com/search.php). This database contains both C-value and chromosome number data. We gathered C-value data for 637 bird species. To complete chromosome number
data, which was extremely limited, we also used data published by Kretschmer et al., (2018).

Body mass data were obtained from Wilman et al., (2014). Brain mass data were compiled from three published sources (Fristoe et al., 2017; Minias & Podlaszczuk 2017; Tsuboi et al., 2018).

Overall, both brain size and genome size data were available for 311 species. Finally, genome size, chromosome number, brain size, and body size data were available for 65 species. All data used in the analyses are available in Supplementary Material 1. Phylogenetic trees used in analyses (see below) are attached as Supplementary Material 2 and 3. Bird order and species names follow Gill et al., (2020).

Data analysis

We computed three single-consensus trees using stringent consensus methods implemented in PAUP* 4.0 (Swofford 2003) from the three sets of 1,000 trees published by Jetz et al., (2012, 2014) downloaded from birdtree.org. The consensus methods used show the tree group sequences only if that grouping appears in all trees in the set. Three consensus trees were used in subsequent statistical analyses. The tree branch lengths were generated from the fitted branch lengths of the 1,000 input trees using the “consensus.edges” function of the phytools package in R (Revell 2012). The trees were visualized with Iroki (Moore et al., 2020) using the ggplot package in R (Wickham 2016), as shown in Figure S1 in Supplementary material 4.

Moreover, the summary statistics on geographic range size, C-value and chromosome number were visualized in Figure 1 using a phylogenetic tree from Kimball et al. (2019). The species for which range size centroid is located below 30° latitude are considered “tropical” species and are depicted in a different color from other species in visualizations.

We performed two sets of analyses: one based on the consensus trees published by Jetz et al., (2012, 2014) and another based on the tree published by Ksepka et al., (2020). We used PGLS models implemented in the nlme package (von Hardenberg & Gonzalez-Voyer 2013; Pinheiro et al., 2019) and used the Brownian motion correlation structure of the model residuals to account for the phylogenetic dependence of species (Münkemüller et al., 2012). Brownian motion is a popular model in comparative biology, because it captures the potential trends of trait evolution under a reasonably wide range of scenarios (Münkemüller et al., 2012; Harmon 2019).

Range sizes of the various bird species (km²) was the dependent variable, while genome size (C-value) and chromosome number were the primary explanatory variables. We also included
following covariates: body mass, relative brain mass, and geographic latitude (absolute values). The relative brain mass residual in the PGLS model was not explained by body mass. These variables are well linked to environmental variability and other species traits. Body mass and relative brain mass were logarithmically transformed. The number of available data varied among the explanatory variables; therefore, we built three models based on the trees published by Jetz et al., (2012, 2014) for explaining range size variation in birds. The first model (637 species) included two explanatory variables, namely genome size and body mass. The second model (311 species) included three explanatory variables, namely genome size, body mass, and relative brain mass. The third model (65 species) included four explanatory variables, namely genome size, chromosome number, body mass, relative brain mass and latitude. Each model was tested against the null model (the model with the intercept alone) using the likelihood ratio test. The Nagelkerke pseudo-R square, calculated in the companion package of R, was used as the measure of model fit (Mangiafico 2020).

Furthermore, we used PPA (von Hardenberg & Gonzalez-Voyer 2013) based on prespecified candidate path models to test for the effects of traits on range variation using the “phylopath” package in R (van der Bijl 2018). This approach allowed us to compare the causal hypotheses regarding the associations among traits, disentangling the direct effects from the indirect ones, while correcting for the non-independence of the trait data due to common ancestry (Santini et al., 2019). In addition, this model accounts for trait multicollinearity (Fig. 2) better than multivariate linear models, because the variance of the response is partitioned among fewer predictors (Gonzalez-Voyer & von Hardenberg 2014). To build paths, we used data from the third model, which contained all explanatory variables. The only difference was that we used raw data on brain mass (logarithmically transformed) because the analysis enables to disentangle the complex relations among variables. A total of 22 path model combinations were built with different configurations of these variables. We used a set of hypotheses depicted by directed acyclic graphs (Fig. 3) to minimize the number of models for testing (Gonzalez-Voyer et al., 2016). The first set of models included the direct impact of each explanatory variable (Fig. 3), and the second set of models included indirect effects. We assumed that (1) the effect of genome size may be mediated by chromosome number, (2) the effect of body mass may be mediated by genome size, (3) the effect of brain mass may be indirect via relative brain mass, and (4) the effect of geographic latitude may be mediated by body mass (Martin 1981). The third
set of models included more complex indirect associations (Fig. 3). Specifically, we assumed
that the effect of body mass may be mediated by both genome size and chromosome number and
that the effect of genome size may be mediated by chromosome number. Finally, these sets of
models were tested against the null model. The sets of models were compared using the C-
statistic Information Criterion corrected for small sample sizes.

All analyses were repeated on the subset of species included in the latest phylogeny
published by Ksepka et al., (2020). However, the sample size was lower. The first PGLS model
(262 species) included two explanatory variables, namely genome size and body mass. The
second model (254 species) included three explanatory variables, namely genome size, body
mass, and relative brain mass. The third model (55 species) included four explanatory variables,
namely genome size, chromosome number, body mass, relative brain mass and latitude. The
PPA was based on the third model with 55 species.

Results

The first PGLS model showed that range size was positively associated with genome size
and latitude but negatively associated with body mass (Table 1; Fig. 4). This model was
statistically different from the null model ($\chi^2 = 13.048, P < 0.001$) and explained 4% of the total
variation in range size. The second PGLS model also revealed that range size was positively
associated with genome size but negatively associated with body mass, and not associated with
relative brain mass and latitude (Table 1). This model was also statistically different from the
null model ($\chi^2 = 11.007, P = 0.008$) and explained 6% of the total variation in range size.
Furthermore, the third PGLS model showed that range size was associated with genome size and
body mass but not with chromosome number, relative brain mass and latitude (Table 1). This
model was statistically different from the null model ($\chi^2 = 12.738, P = 0.002$) and explained
18% of the total variation in range size. In PPA, the models with indirect simple and indirect
complex effects gained the highest support (Table 2). Based on the estimated coefficients,
genome size had a significant and independent effect (confidence intervals not overlapping with
zero) on range size (Fig. 5).
Analysis based on the tree published by Ksepka et al., (2020) yielded similar results (Table S1 and Fig. S2 in Supplementary Material 4). However, geographic latitude was significant in all models examined. Moreover, in second model the relative brain mass had positive effect on geographic range size (Table S1). In third model the number of chromosomes had negative effect on the range size and the effect of the genome size was non-significant (Table S1). However, the third model with all explanatory variables suffered due to small sample size as revealed by running fourth model with the effect of genome size only (Table S1). Based on these limited data, PPA indicated that range size was positively associated with geographic latitude but negatively associated with chromosome number (Table S2 and Fig. S2 in Supplementary Material 4).

Discussion

Large-scale patterns of spatial variation in species’ geographic ranges are central to many fundamental questions in macroecology. However, the global nature of these patterns remains contentious. The present study confirmed our hypothesis that in birds, genome size is weakly but positively associated with geographic range size. Moreover, analysis on phylogenetic tree from Ksepka et al. (2020) showed that range size may be negatively correlated with chromosome numbers. Birds represent an example of a group in which genome size is correlated with active speciation. The amount of DNA gained by transposable element expansion is counteracted by DNA loss from large segmental deletions (Kapusta et al., 2017; Zhang et al., 2014). Thus, genome size regulation (Fisher et al., 2014) is perhaps more important to adaptation than genome size itself. Furthermore, the effect of genome size on geographic range size is not easy to predict, considering that it largely represents the dynamic balance between positive and negative selection on genome size. According to Lynch & Conery (2003), the ineffectiveness of selection in species with a low effective population size is key to genome evolution. Large organisms have lower population sizes than small ones and hence a lower effective population size. The effective population size determines whether natural selection can maintain functional DNA sequences in the face of deleterious mutations. It is almost impossible for a deleterious mutation to spread when the effective population size is large; thus, it may prevent genome enlargement. Interestingly, the positive association between population size and geographic range size is well-
documented (Gaston & Blackburn 1996). Thus, these contrasting forces may be the reason
statistical models in this study explained only a small proportion of variation in range size.
However, our results are not different from the explained variances generally reported in
ecological research. According to Møller & Jennions (2002), statistical models can explain
between 2.5% and 5.4% of variation in ecological studies. Moreover, there may be additional
explanations for the variation in range size in birds, which are mostly linked to environmental
constraints, such as climate, geographic location, and habitat (Orme et al., 2006; Laube et al.,
2014; Zhang et al., 2014; Sayol et al., 2016). Our results support prediction that the range size
increase with latitude. This finding is in line with the Rapoport’s rule which states that there is a
positive latitudinal gradient in latitudinal range extent (Rapoport 1982; Stevens 1989). Despite
there is a criticism of this rule stating that this is a local phenomenon occurring only on the
northern Hemisphere above a latitude of about 40-50°N (Ruggiero & Lawton 1998), there are
several studies supporting the Rapoport’s rule, e.g. in amphibians (Whitton et al., 2012), birds
(Dyer et al., 2020) and mammals (Arita et al., 2005).

Interestingly, we found that body mass was negatively correlated with range size in
multivariate models. This result contradicts most previous findings, which are considered the
paradigm of macroecology (Cambefort 1994; Gaston & Blackburn 1996; Gaston & Blackburn
2000). However, Gaston & Blackburn (1996) used range size data of limited quality (generalized
range maps); therefore, they may have greatly underestimated the range of several species with
very small distributions. Hence, such an association should be investigated in more detail in
additional taxa, because this knowledge may change our understanding of the role of body size in
shaping range sizes. Body size depends on genome size (rather than vice versa); thus, genetic
factors may be the primary causative variables, while body mass may be linked indirectly with
species range.

Furthermore, we did not find effect of relative brain mass on range size, contrary to the
previous reports of a positive association between environmental variation and brain size (Sayol
et al., 2016). The effect was significant in one analysis based on Ksepka et al. (2020) but was not
supported by PPA. Larger brains indicate higher cognitive ability (information processing) under
strong selection (Reader & Laland 2002; Sol et al., 2005). The possible explanation for this is
that on a geographic scale, environmental variation may be too high for birds to adapt their
cognitive skills. In this case, adaptations to dynamic conditions would evolve, which may be
linked with genome size.

Study limitations

Several issues should be taken into consideration when interpreting our results. One of the
great challenges in recent studies of macroecological patterns has been how to explain the
highly aggregated distribution of species with very small geographic ranges in specific tropical
regions (for example, oroclines, locations near the edges of continental plates, or archipelagos
[Rahbek et al., 2007, 2019; Jønsson et al., 2017]). Interestingly, 50% of the avian species with
very small geographic ranges are exclusively found at latitudes below 30°. Unfortunately,
however, the genome data for these species are poorly represented. Hence, the results depend
largely on geographic sampling. Our results are biased toward species with large-to-moderate
geographic ranges, neglecting numerous tropical species with very small ranges. This bias may
also explain the negative association between range size and body size. Another bias (or
confounding factor) may be that flight ability (aerial foraging) has been found to correlate with a
small genome size (Andrews et al., 2009; Kapusta et al., 2017); However, flight ability may also
affect range size. As the genome size may be increased by the replication of transposable
elements it may be also decreased by large deletions indicating that counteracting selective
forces shape bird genome size (Kapusta et al., 2017; Zhang et al., 2014). Moreover, our sample
size for analyses was limited by the availability of data on chromosome number. Thus, data on
avian karyotypes and other traits potentially related to range should be included in future studies.
Statistical methods we used assume that relationships are linear, which is not necessarily an
optimal assumption (Quader et al., 2004). Phylogenetic comparative methods can fail to detect
coevolution when the underlying relationships among traits are nonlinear (Quader et al., 2004).
However, it is difficult to include nonlinear methods in phylogenetically corrected statistics,
specifically PPA. We overcame this problem by logarithmic transformation of body mass and
brain size data. Moreover, geographic latitude was included as an absolute value to allow for
linear modeling.

We used two avian phylogenies. The first was proposed by Jetz et al., (2012, 2014) and
included all taxa for which there are no real-time data. In that tree, there are parts of the topology
for taxa with no data that have 100% support (Hosner et al., 2015), which likely reflects the
difficulty of running the Markov chain Monte Carlo algorithm long enough to adequately sample
the posterior distribution when a large number of taxa are included. Meanwhile, the tree
presented by Ksepka et al., (2020) included fewer species, omitting some avian orders (such as
Casuariiformes and Ciconiiformes). Analysis based on this tree had a lower sample size and thus
a lower power, particularly when building models with all explanatory variables. Analyses with
both trees yielded slightly different results when the sample size was small. This indicate that
further research on avian phylogeny based on genome sequences with inclusion of as many taxa
as possible are required. In addition, species ranges are not constant, and the range data used
have other well-known limitations, however not better options exist at that scale of study.

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References

Andrews CB, Mackenzie SA, Gregory TR. 2009. Genome size and wing parameters in passerine
birds. Proceedings of the Royal Society B. 276: 55–61 DOI: https://doi.org/10.1098/rspb.2008.1012.

Arita HT, Rodríguez P, Vázquez-Domínguez E. 2005. Continental and regional ranges of North
American mammals: Rapoport’s rule in real and null words. Journal of Biogeography 32: 961–
971 DOI: https://doi.org/10.1111/j.1365-2699.2005.01276.x.

Arnqvist G, Sayadi A, Immonen E, Hotzy C, Rankin D, Tuda M, Hjelmen CE, Johnston JS.
2015. Genome size correlates with reproductive fitness in seed beetles. Proceedings of the Royal
Society B. 282: 20151421 DOI: https://doi.org/10.1098/rspb.2015.1421.
Barberán A, Ramirez KS, Leff JW, Bradford MA, Wall DH, Fierer N. 2014. Why are some microbes more ubiquitous than others? Predicting the habitat breadth of soil bacteria. *Ecology Letters* 17: 794–802 DOI: https://doi.org/10.1111/ele.12282.

Benetzen JL, Kellogg EA. 1997. Do Plants Have a One-Way Ticket to Genomic Obesity? *The Plant Cell* 9: 1509–1514 DOI: https://doi.org/10.1105/tpc.9.9.1509.

BirdLife International. 2019. Important Bird Areas factsheet: Isla Diego de Almagro. Downloaded from http://www.birdlife.org (accessed 20 November 2019).

Blackmon H, Ross L, Bachtrog D. 2017. Sex Determination, Sex Chromosomes, and Karyotype Evolution in Insects. *Journal Heredity* 108: 78–93 DOI: https://doi.org/10.1093/jhered/esw047.

Böhning-Gaese K, Caprano T, van Ewijk K, Veith M. 2006. Range Size: Disentangling Current Traits and Phylogenetic and Biogeographic Factors. *American Naturalist* 167: 555–567 DOI: https://doi.org/10.1086/501078.

Burleigh JG, Kimball RT, Braun EL (2015) Building the avian tree of life using a large-scale, sparse supermatrix. *Molecular Phylogenetics and Evolution* 84: 53–63 DOI: https://doi.org/10.1016/j.ympev.2014.12.003.

Cambefort Y. 1994. Body-size, abundance, and geographical distribution of Afrotropical dung beetles (Coleoptera, Scarabaeidae). *Acta Oecologica* 15: 165–179.

Cavalier-Smith T. 1978. Nuclear volume control by nucleoskeletal DNA, selection for cell volume and cell growth rate, and the solution of the DNA C-value paradox. *Journal of Cell Science* 34: 247–278.

Charlesworth B, Barton N. 2004. Genome Size: Does Bigger Mean Worse? *Current Biology* 14: R233–R235 DOI: https://doi.org/10.1016/j.cub.2004.02.054.

Choudoir MJ, Barberán A, Menninger HL, Dunn RR, Fierer N. 2018. Variation in range size and dispersal capabilities of microbial taxa. *Ecology* 99: 322–334 DOI: https://doi.org/10.1002/ecy.2094.
Degrandi TM, Barcellos SA, Costa AL, Garnero ADV, Hass I, Gunski RJ. 2020. Introducing the Bird Chromosome Database: An Overview of Cytogenetic Studies in Birds. Cytogenetic and Genome Research 160: 199–205 DOI: https://doi.org/10.1159/000507768.

Dyers EE, Redding DW, Cassey P, Collen B, Blackburn TM. 2020. Evidence for Rapoport’s rule and latitudinal patterns in the global distribution and diversity of alien bird species. Journal of Biogeography 47: 1362–1372 DOI: https://doi.org/10.1111/jbi.13825.

Edmunds NB, Laberge F, McCann KS. 2016. A role for brain size and cognition in food webs. Ecology Letters 19: 948–955 DOI: https://doi.org/10.1111/ele.12633.

Elliott TA, Gregory TR. 2015. What’s in a genome? The C-value enigma and the evolution of eukaryotic genome content. Philosophical Transactions of the Royal Society B. 370: 20140331 DOI: https://doi.org/10.1098/rstb.2014.0331.

Emery NJ. 2006. Cognitive ornithology: the evolution of avian intelligence. Philosophical Transactions of the Royal Society B. 361: 23–43 DOI: https://doi.org/10.1098/rstb.2005.1736.

Fristoe TS, Iwaniuk AN, Botero CA. 2017. Big brains stabilize populations and facilitate colonization of variable habitats in birds. Nature Ecology and Evolution 1: 1706–1715 DOI: https://doi.org/10.1038/s41559-017-0316-2.

Garcia-Barros E, Romo Benito H. 2010. The relationship between geographic range size and life history trait: is biogeographic history uncovered? A test using the Iberian butterflies Ecography 33: 392–401 DOI: https://doi.org/10.1111/j.1600-0587.2010.06269.x.

Gaston KJ. 2003. The Structure and Dynamics of Geographic Ranges. Oxford: Oxford University Press.

Gaston KJ, Blackburn TM. 1996. Global Scale Macroecology: Interactions between Population Size, Geographic Range Size and Body Size in the Anseriformes. Journal of Animal Ecology 65: 701–714 DOI: https://doi.org/10.2307/5669.

Gaston KJ, Blackburn TM. 2000. Pattern and Process in Macroecology. Oxford: Blackwell Publishing.
Gill F, Donsker D, Rasmussen P. 2020. IOC World Bird List (v10.2). DOI: 10.14344/IOC.ML.10.2. https://www.worldbirdnames.org/

Gillies CS, St. Clair CC. 2010. Functional responses in habitat selection by tropical birds moving through fragmented forest. Journal of Applied Ecology 47:182–190. DOI: https://doi.org/10.1111/j.1365-2664.2009.01756.x.

Gonzalez-Voyer A, Gonzalez-Suarez M, Vila C, Revilla E. 2016 Larger brain size indirectly increases vulnerability to extinction in mammals. Evolution 70: 1364–1375 DOI: https://doi.org/10.1111/evo.12943.

Gonzalez-Voyer A, von Hardenberg A. 2014. An introduction to phylogenetic path analysis. In: Garamszegi LZ, ed. Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology. Berlin, Heidelberg: Springer-Verlag, 201–229.

Gregory TR. 2002 Genome size and developmental complexity. Genetica 115: 131–146 DOI: https://doi.org/10.1023/A:1016032400147.

Gregory TR. (ed) 2005. The Evolution of the Genome. San Diego: Elsevier.

Gregory TR, Hebert PD. 1999. The modulation of DNA content: proximate causes and ultimate consequences. Genome Research 9: 317–324 DOI: https://doi.org/10.1101/gr.9.4.317

Guo QF, Kato M, Ricklefs RE. 2003. Life history, diversity and distribution: a study of Japanese pteridophytes. Ecography 26: 129–138 DOI: https://doi.org/10.1034/j.1600-0587.2003.03379.x.

Hackett SJ, Kimball RT, Reddy S, Bowie RCK, Braun EL, Braun MJ, Chojnowski JL, Cox WA, Han K-L, Harshman J, Huddleston CJ, Marks BD, Miglia KJ, Moore WS, Sheldon FH, Steadman DW, Witt CC, Yuri T. 2008. A Phylogenomic Study of Birds Reveals Their Evolutionary History. Science 320: 1763–1768 DOI: https://doi.org/10.1126/science.1157704.

Harmon LJ. 2019. Phylogenetic Comparative Methods. CC-BY 2019. Available from: https://lukejharmann.github.io/pcm/pdf/phylogeneticComparativeMethods.pdf.

Hosner PA, Braun EL, Kimball RT. 2015. Land connectivity changes and global cooling shaped the colonization history and diversification of New World quail (Aves: Galliformes:

PeerJ reviewing PDF | (2020:07:50951:2:0:NEW 5 Jan 2021)
Odontophoridae). *Journal of Biogeography* **42**: 1883–1895 DOI: https://doi.org/10.1111/jbi.12555.

Hou Y, Lin S. 2009. Distinct Gene Number-Genome Size Relationships for Eukaryotes and Non-Eukaryotes: Gene Content Estimation for Dinoflagellate Genomes. *PLoS ONE* **4**(9): e6978 DOI: https://doi.org/10.1371/journal.pone.0006978.

Hsu TC. 1975. A possible function of constitutive heterochromatin: the bodyguard hypothesis. *Genetics* **79** (Suppl.): 137–150.

Janssen A, Colmenares SU, Karpen GH. 2018. Heterochromatin: Guardian of the genome. *Annual Review of Cell and Developmental Biology* **34**: 265–288 DOI: https://doi.org/10.1146/annurev-cellbio-100617-062653.

Jarvis ED, Mirarab S, Aberer AJ, Li B, Houde P, Li C, Ho SYW, Faircloth BC, Nabholz B, Howard JT, Suh A, Weber CC, da Fonseca RR, Li J, Zhang F, Li H, Zhou L, Narula N, Liu L, Ganapathy G, Boussau B, Bayzid MS, Zavidovych V, Subramanian S, Gabaldon T, Capella-Gutierrez S, Huerta-Cepas J, Rekepalli B, Munch K, Schierup M, Lindow B, Warren WC, Ray D, Green RE, Bruford MW, Zhan X, Dixon A, Li S, Li N, Huang Y, Derryberry EP, Bertelsen MF, Sheldon FH, Brumfield RT, Mello CV, Lovell PV, Wirthlin M, Schneider MPC, Prosdocimi F, Samaniego JA, Velazquez AMV, Alfaro-Nunez A, Campos PF, Petersen B, Sicheritz-Ponten T, Pas A, Bailey T, Scofield P, Bunce M, Lambert DM, Zhou Q, Perelman P, Driskell AC, Shapiro B, Xiong Z, Zeng Y, Liu S, Li Z, Liu B, Wu K, Xiao J, Yinqi X, Zheng Q, Zhang Y, Yang H, Wang J, Smeds L, Rheindt FE, Braun M, Fjeldsa J, Orlando L, Barker FK, Jonsson KA, Johnson W, Koepfli K-P, O’Brien S, Haussler D, Ryder OA, Rahbek C, Willerslev E, Graves GR, Glenn TC, McCormack J, Burt D, Ellegren H, Alstrom P, Edwards SV, Stamatakis A, Mindell DP, Cracraft J, Braun EL, Warnow T, Jun W, Gilbert MTP, Zhang G. 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* **346**:1320–1331 DOI: https://doi.org/10.1126/science.1253451.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. *Nature* **491**: 444–448 DOI: https://doi.org/10.1038/nature11631.
Jetz W, Thomas GH, Joy JB, Hartmann K, Redding D, Mooers AO. 2014. Global Distribution and Conservation of Evolutionary Distinctness in Birds. *Current Biology* **24**: 1–12 DOI: https://doi.org/10.1016/j.cub.2014.03.011.

John B, Miklos GLG. 1988. *The Eukaryotic Genome in Development and Evolution*, Allen & Unwin.

Jönnson K. A. Borregaard M. K. Carstensen D. W. Hansen L. A. Kennedy J. D. Machac A. Marki P. Z. Fjeldså J. Rahbek C. 2017. Biogeography and biotic assembly of Indo-Pacific corvid passerine bird diversity. *Annual Review in Ecology, Evolution and Systematics* **48**: 231–253 DOI: https://doi.org/10.1146/annurev-ecolsys-110316-022813.

Kapusta A, Suh A, Fescotte C. 2017. Dynamics of genome size evolution in amniotes. *Proceedings of the National Academy of Sciences USA*. **114** *(8)*: E1460–E1469 DOI: https://doi.org/10.1073/pnas.1616702114.

King M. 1995 *Species Evolution*. Cambridge: Cambridge University Press.

Khaliq I, Fritz SA, Prinzinger R, Pfenninger M, Böhning-Gaese K, Hof C. 2015. Global variation in thermal physiology of birds and mammals: evidence for phylogenetic niche conservatism only in the tropics. *Journal of Biogeography* **42**: 2187–2196 DOI: https://doi.org/10.1111/jbi.12573.

Kretschmer R, Ferguson-Smith M, de Oliveira E. 2018. Karyotype Evolution in Birds: From Conventional Staining to Chromosome Painting. *Genes* **9**: 181 DOI: https://doi.org/10.3390/genes9040181.

Ksepka DT, Balanoff AM, Smith NA, Bever GS, Bhullar B-AS, Bourdon E, Braun EL, Burleigh JG, Clarke JA, Colbert MW, Corfield JR, Degrange FJ, De Pietri VL, Early CM, Field DJ, Gignac PM, Gold MEL, Kimball RT, Kawabe S, Lefebvre L, Marugán-Lobón J, Mongle CS, Morhardt A, Norell MA, Ridgely RC, Rothman RS, Scofield RP, Tambussi CP, Torres CR, van Tuinen M, Walsh SA, Watanabe A, Witmer LM, Wright AK, Zanno LE, Jarvis ED, Smaers JB.
2020. Tempo and Pattern of Avian Brain Size Evolution. *Current Biology* **30**: 2026-2036.e3

DOI: https://doi.org/10.1016/j.cub.2020.03.060.

Laube I, Korntheuer H, Schwager M, Trautmann S, Rahbek C, Böhning-Gaese K. 2013. Towards a more mechanistic understanding of traits and range sizes. *Global Ecology and Biogeography* **22**: 233–241 DOI: https://doi.org/10.1111/j.1466-8238.2012.00798.x.

Lee-Yaw JA, Irwin DE. 2012. Large geographic range size reflects a patchwork of divergent lineages in the long-toed salamander (*Ambystoma macrodactylum*). *Journal of Evolutionary Biology* **25**: 2276–2287 DOI: https://doi.org/10.1111/j.1420-9101.2012.02604.x.

Lefèbure T, Morvan C, Malard F, François C, Konecny-Dupré L, Guéguen L, Weiss-Gayet M, Seguin-Orlando A, Ermini L, Sarkissian CD, Charrier NP, Eme D, Mermillod-Blondin F, Duret L, Vieira C, Orlando L, Douady CJ. 2017. Less effective selection leads to larger genomes. *Genome Research* **27**: 1016–1028 DOI: https://doi.org/10.1101/gr.212589.116.

Lester SE, Ruttenberg BI, Gaines SD, Kinlan BP. 2007. The relationship between dispersal ability and geographic range size. *Ecology Letters* **10**: 745–758 DOI: https://doi.org/10.1111/j.1461-0248.2007.01070.x.

Levin DA. 2002. The role of chromosomal change in plant evolution. Oxford, UK: Oxford University Press.

Liedtke HC, Gower DJ, Wilkinson M, Gomez-Mestre I. 2018. Macroevolutionary shift in the size of amphibian genomes and the role of life history and climate. *Nature Ecology and Evolution* **2**: 1792 DOI: https://doi.org/10.1038/s41559-018-0674-4.

Lucek K. 2018. Evolutionary Mechanisms of Varying Chromosome Numbers in the Radiation of Erebia Butterflies. *Genes* **9**(3): 166 DOI: https://doi.org/10.3390/genes9030166.

Lynch M, Conery JS. 2003. The Origins of Genome Complexity. *Science* **302**: 1401–1404 DOI: https://doi.org/10.1126/science.1089370.

Mangiafico S. 2020. rcompanion: Functions to Support - Extension Education Program Evaluation. R package version 2.3.25. https://CRAN.R-project.org/package=rcompanion
Martin RD. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* **293**: 57–60 DOI: https://doi.org/10.1038/293057a0.

Martinez PA, Jacobina UP, Fernandes RV, Brito C, Penone C, Amado TF, Fonseca CR, Bidau CJ. 2017. A comparative study on karyotypic diversification rate in mammals. *Heredity* **118**(4): 366–373 DOI: https://doi.org/10.1038/hdy.2016.110.

Minias P, Podlaszczuk P. 2017. Longevity is associated with relative brain size in birds. *Ecology and Evolution* **7**: 3558–3566 DOI: https://doi.org/10.1002/ece3.2961.

Moore RM, Harrison AO, McAllister SM, Polson SW, Wommack KE. 2020. Iroki: automatic customization and visualization of phylogenetic trees. *PeerJ* **8**: e8584 DOI: https://doi.org/10.7717/peerj.8584.

Møller AP, Jennions MD. 2002. How much variance can be explained by ecologists and evolutionary biologists? *Oecologia* **132**: 492–500 DOI: https://doi.org/10.1007/s00442-002-0952-2.

Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schifers K, Thuiller W. 2012. How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* **3**: 743–756 DOI: https://doi.org/10.1111/j.2041-210X.2012.00196.x.

Navarrete AF, Reader SM, Street SE, Whalen A, Laland KN. 2016. The coevolution of innovation and technical intelligence in primates. *Philosophical Transactions of the Royal Society B.* **371**: 20150186 DOI: https://doi.org/10.1098/rstb.2015.0186.

Newsome TM, Wolf C, Nimmo DG, Keller Kopf R, Ritchie EG, Smith FA, Ripple WJ. 2019. Constraints on vertebrate range size predict extinction risk. *Global Ecology and Biogeography* **29**: 76–86 DOI: https://doi.org/10.1111/geb.13009.

Orme CDL, Davies RG, Olson VA, Thomas GH, Ding T-S, Rasmussen PC, Ridgely RS, Stattersfield AJ, Bennett PM, Owens IPF, Blackburn TM, Gaston KJ. 2006. Global patterns of geographic range size in birds. *PLoS Biology* **4**(7): e208 DOI: https://doi.org/10.1371/journal.pbio.0040208.

Petrov DA. 2001. Evolution of genome size: new approaches to an old problem. *Trends in Genetics* **17**: 23–28 DOI: https://doi.org/10.1016/s0168-9525(00)02157-0.
Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2019. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-142, https://CRAN.R-project.org/package=nlme

Pandit MK, White SM, Pocock MJO. 2014. The contrasting effects of genome size, chromosome number and ploidy level on plant invasiveness: a global analysis. New Phytologist 203: 697–703 DOI: https://doi.org/10.1111/nph.12799.

QGIS Development Team. 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

Quader S, Isvaran K, Hale RE, Miner BG, Seavy NE. 2004. Nonlinear relationships and phylogenetically independent contrasts. Journal of Evolutionary Biology 17: 709–715 DOI: https://doi.org/10.1111/j.1420-9101.2004.00697.x

Rahbek C, Gotelli NJ, Colwell RK, Entsminger GL, Rangel TFLVB, Graves GR. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. Proceedings of the Royal Society B: Biological Sciences 274: 165–174 DOI: https://doi.org/10.1098/rspb.2006.3700.

Rahbek C, Borregaard MK, Colwell RK, Dalsgaard B, Holt BG, Morueta-Holme N, Nogues-Bravo D, Whittaker RJ, Fjeldså J. 2019. Humboldt’s enigma: What causes global patterns of mountain biodiversity? Science 365: 1108–1113 DOI: https://doi.org/10.1126/science.aax0149.

Rapoport EH. 1982. Aerography: Geographical Strategies of Species. New York> Pergamon press.

Ravilious C, Goodman L, Bodin B, Runsten L, Osti M. 2015. Using spatial information to support decisions on safeguards and multiple benefits for REDD+. Step-by-step tutorial v1.0: Extracting and processing IUCN Red List species data using a vector method in a combination of QGIS 1.8 and 2.8. Prepared on behalf of the UN-REDD Programme. UNEP World Conservation Monitoring Centre, Cambridge, UK.

Reader SM, Laland KN. 2002 Social intelligence, innovation, and enhanced brain size in primates. Proceedings of the National Academy of Sciences USA 99(7): 4436–4441 DOI: https://doi.org/10.1073/pnas.062041299.
Revell LJ. 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223 DOI: https://doi.org/10.1111/j.2041-210X.2011.00169.x.

Ruggiero A, Lawton JH. 1998. Are there latitudinal and altitudinal Rapoport effects in the geographic ranges of Andean passerine birds? *Biological Journal of the Linnean Society* **63**: 283–304 DOI: https://doi.org/10.1006/bijl.1997.0190.

Santini L, González-Suárez M, Russo D, Gonzalez-Voyer A, von Hardenberg A, Ancillotto L. 2019. One strategy does not fit all: Determinants of urban adaptation in mammals. *Ecology Letters* **22**: 365–376.

Sayol F, Maspons J, Lapiedra O, Iwaniuk AN, Székely T, Sol D. 2016. Environmental variation and the evolution of large brains in birds. *Nature Communications* **7**: 13971 DOI: https://doi.org/10.1038/ncomms13971.

Sessions SK, Larson A. 1987. Developmental correlates of genome size in Plethodontid salamanders and their implications for genome evolution. *Evolution* **41**: 1239–1251 DOI: https://doi.org/10.1111/j.1558-5646.1987.tb02463.x.

Smith BT, Bryson RW, Houston DD, Klicka J. 2012. An asymmetry in niche conservatism contributes to the latitudinal species diversity gradient in New World vertebrates. *Ecology Letters* **15**: 1318–1325 DOI: https://doi.org/10.1111/j.1461-0248.2012.01855.x.

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences USA* **102**: 5460–5465 DOI: https://doi.org/10.1073/pnas.0408145102.

Stevens GC. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist* **133**: 240–256.

Swofford DL. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Tsuboi MW, Van der B, Kopperud BT, Erritzøe J, Voje KL, Kotrschal A, Yopak KE, Collin SP, Iwaniuk AN, Kolm N. 2018. Breakdown of brain–body allometry and the encephalization of
birds and mammals. *Nature Ecology and Evolution* **2**: 1492–1500 DOI: https://doi.org/10.1038/s41559-018-0632-1.

van der Bijl W. 2018. *phylopath*: Easy phylogenetic path analysis in R. *PeerJ* **6**: e4718 DOI: https://doi.org/10.7717/peerj.4718.

Vinogradov AE. 1997. Nucleotypic effect in homeotherms: body-mass independent resting metabolic rate of passerine birds is related to genome size. *Evolution* **51**: 220–225 DOI: https://doi.org/10.1111/j.1558-5646.1995.tb04451.x.

Vinogradov AE. 1998. Genome size and GC-percent in vertebrates as determined by flow cytometry: the triangular relationship. *Cytometry* **31**: 100–109 DOI: https://doi.org/10.1002/(sici)1097-0320(19980201)31:2<100::aid-cyto5>3.0.co;2-q.

von Hardenberg A, Gonzalez-Voyer A. 2013. Disentangling evolutionary cause-effect relationships with phylogenetic confirmatory path analysis. *Evolution* **67**: 378–387 DOI: https://doi.org/10.1111/j.1558-5646.2012.01790.x.

Wang N, Kimball RT, Braun EL, Liang B, Zhang Z. 2017. Ancestral range reconstruction of Galliformes: the effects of topology and taxon sampling. *Journal of Biogeography* **44**: 122–135 DOI: https://doi.org/10.1111/jbi.12782.

Warchałowska-Śliwa E, Maryańska-Nadachowska A, Grzywacz B, Karamysheva T, Lehmann AW, Lehmann GUC, Heller K-G. 2011. Changes in the numbers of chromosomes and sex determination system in bushcrickets of the genus *Odontura* (Orthoptera, Tettigoniidae, Phaneropterinae). *European Journal of Entomology* **108**: 183–195 DOI: https://doi.org/10.14411/eje.2011.025.

Whitton FJS, Purvis A, Orme CDL, Olalla-Tarraga MA. 2012. Understanding global patterns in amphibian geographic range size: Does Rapoport rule? *Global Ecology and Biogeography* **21**: 179–190 DOI: https://doi.org/10.1111/j.1466-8238.2011.00660.x.

Wickham H. 2016. *ggplot2*: Elegant Graphics for Data Analysis. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.
Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira M.M, Jetz W. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95**: 2027 DOI:10.1890/13-1917.1.

Winger BM, Auteri GG, Pegan TM, Weeks BC. 2019. A long winter for the Red Queen: Rethinking the evolution of seasonal migration. *Biological Reviews* **94**: 737-753 DOI: https://doi.org/10.1111/brv.12476.

Wyngaard GA, Rasch EM, Manning NM, Gasser K, Domangue R. 2005. The relationship between genome size, development rate, and body size in copepods. *Hydrobiologia* **532**: 123–137 DOI: https://doi.org/10.1007/s10750-004-9521-5.

Xia X. 1995. Body temperature, rate of biosynthesis, and evolution of genome size. *Molecular Biology and Evolution* **12**: 834–842 DOI: https://doi.org/10.1093/oxfordjournals.molbev.a040260.

Yu JP, Liu W, Mai CL, Liao WB. 2019. Genome size variation is associated with life-history traits in birds. *Journal of Zoology* **310**: 255–260 DOI: https://doi.org/10.1111/jzo.12755.

Zamudio KR, Bell RC, Mason NA. 2016. Phenotypes in phylogeography: species’ traits, environmental variation, and vertebrate diversification. *Proceedings of the National Academy of Sciences USA* **113**: 8041–8048.

Zhang G, Li C, Li Q, Li B, Larkin DM, Lee C, Storz JF, Antunes A, Greenwold MJ, Meredith RW, Odeen A, Cui J, Zhou Q, Xu L, Pan H, Wang Z, Jin L, Zhang P, Hu H, Yang W, Hu J, Xiao J, Yang Z, Liu Y, Xie Q, Yu H, Lian J, Wen P, Zhang F, Li H, Zeng Y, Xiong Z, Liu S, Zhou L, Huang Z, An N, Wang J, Zheng Q, Xiong Y, Wang G, Wang B, Wang J, Fan Y, da Fonseca RR, Alfaro-Nunez A, Schubert M, Orlando L, Mourier T, Howard JT, Ganapathy G, Pfenning A, Whitney O, Rivas MV, Hara E, Smith J, Farre M, Narayan J, Slavog G, Romanov MN, Borges R, Machado JP, Khan I, Springer MS, Gatesy J, Hoffmann FG, Opazo JC, Hastad O, Sawyer RH, Kim H, Kim K-W, Kim HJ, Cho S, Li N, Huang Y, Bruford MW, Zhan X, Dixon A, Bertelsen MF, Derryberry E, Warren W, Wilson RK, Li S, Ray DA, Green RE, O’Brien SJ, Griffin D, Johnson WE, Haussler D, Ryder OA, Willerslev E, Graves GR, Alstrom P, Fjeldsa J, Mindell DP, Edwards SV, Braun EL, Rahbek C, Burt DW, Houde P, Zhang Y, Yang H, Wang J, Jarvis ED, Gilbert MTP, Wang J, Ye C, Liang S, Yan Z, Zepeda ML, Campos PF, Velazquez
AMV, Samaniego JA, Avila-Arcos M, Martin MD, Barnett R, Ribeiro AM, Mello CV, Lovell PV, Almeida D, Maldonado E, Pereira J, Sunagar K, Philip S, Dominguez-Bello MG, Bunce M, Lambert D, Brumfield RT, Sheldon FH, Holmes EC, Gardner PP, Steeves TE, Stadler PF, Burge SW, Lyons E, Smith J, McCarthy F, Pitel F, Rhoads D, Froman DP. 2014. Comparative Genomics Reveals Insights into Avian Genome Evolution and Adaptation. Science 346: 1311–1320 DOI: https://doi.org/10.1126/science.1251385.
Figure 1

A summary statistics of the studied variables

The distribution of bird (A) genome size, (B) number of chromosomes, and (C) geographic range size on the phylogenetic tree. The phylogenetic tree is from Kimball et al. (2019). Bars are means with standard deviations. Sample size (number of species) is given next to each bar. NA indicates that data was not available. Sample size for the geographic range size is the same as for the genome size.
Figure 2

Associations among the explanatory variables revealed by phylogenetic generalized least squares (fitted red line)

Size of the dots is scaled according to geographic range size. The species for which geographic range centroid is located below 30° latitude are considered “tropical” species (orange dots) in contrast to other species (blue dots). Dots are transparent for better visibility of overlapping data. Statistical significance is presented along with sample size.
Figure 3

Competing models in the phylogenetic confirmatory path analysis

Competing models for testing the associations of geographic range size (Range) with genome size, chromosome number (Chromosomes), body mass, relative brain mass and latitude in birds
Figure 4

Associations of geographic range size with (A) genome size (B) body mass of birds, and (C) geographic latitude

Fitted lines (red) are derived from the phylogenetic generalized least squares models. The effect of body mass and latitude on the residual range size (residuals not explained by genome size) is depicted. Further explanations: see Figure 2
Figure 5

Results from the phylogenetic confirmatory path analysis

Test supporting causal model with standardized path coefficients (A). Standardized coefficients with 95% confidence intervals (CIs) for explanatory variables associated with geographic range size of birds (B)
A

Geographic latitude

Chromosomes

Body mass

Brain mass

Range

B

Genome size → Range

Geographic latitude → Range

Brain mass → Range

Chromosomes → Range

Body mass → Range

standardized regression coefficient ± CI
Table 1 (on next page)

Phylogenetic generalized least squares models testing association among geographic species ranges in birds and genome size, chromosome number, body mass, relative brain mass and latitude.

Three models differed by available sample size for each explanatory variable. Statistically significant effects have emboldened P-values.
| Effect            | estimate  | SE        | t    | P     |
|-------------------|-----------|-----------|------|-------|
| (Intercept)       | 2947223.7 | 13563675.8|0.217| 0.828 |
| Genome size       | 11347387.5| 3810612.2 |2.978| **0.003** |
| Body mass         | -1666844.5| 792465.3  |-2.103| **0.036** |
| Geographic latitude| 107082.4  | 34917.7   |3.067| **0.002** |

| Effect            | estimate  | SE        | t    | P     |
|-------------------|-----------|-----------|------|-------|
| (Intercept)       | 1282122.5 | 17644249.3|0.073| 0.942 |
| Genome size       | 16502711.4| 5846290.2 |2.823| **0.005** |
| Body mass         | -2265842.6| 1127589.4 |-2.009| **0.045** |
| Brain mass (residual)| -1224487.9| 5200002.4 |-0.235| 0.814 |
| Geographic latitude| 27604.6   | 57284.6   |0.4882| 0.630 |

| Effect            | estimate  | SE        | t    | P     |
|-------------------|-----------|-----------|------|-------|
| (Intercept)       | 25833067.5| 31459858.8|0.821| 0.415 |
| Genome size       | 29848628.7| 11134362.6|2.681| **0.009** |
| Chromosome number | -345377.8 | 276973.9  |-1.247| 0.217 |
| Body mass         | -3923399.6| 1685932.1 |-2.327| **0.023** |
| Brain mass (residual)| 264551.6  | 8961357.9 |0.030| 0.976 |
| Geographic latitude| 25833067.5| 31459858.8|0.821| 0.415 |
Table 2 (on next page)

Results of the phylogenetic confirmatory path analysis

Different sets of models are compared (see Figure 3) Explanations: $k$ - independence claims made by the model, $q$ - the number of parameters, $C$ - the C statistic, $P$ - p-value for $C$, $CICc$ - the C-statistic information criterion corrected for small sample sizes, $\Delta CICc$ - the difference in $CICc$ with the top model, $l$ - the associated relative likelihoods, $w$ - $CICc$ weights ($w$). A significant $p$ indicates that the available evidence rejects the model.
Table 2.

| Model         | k  | q  | C     | p  | CICc | ΔCICc | l   | w  |
|---------------|----|----|-------|----|------|-------|-----|----|
| indirect simple | 6  | 15 | 13.029 | 0.367 | 52.824 | 0.000 | 1.000 | 0.853 |
| indirect complex | 4  | 17 | 9.323  | 0.316 | 56.345 | 3.520 | 0.172 | 0.147 |
| direct        | 10 | 11 | 93.275 | 0.000 | 120.256 | 67.431 | 0.000 | 0.000 |
| null          | 15 | 6  | 113.251 | 0.000 | 126.700 | 73.875 | 0.000 | 0.000 |