

Electronic Appendix to the Manuscript**“Why are there so few smart mammals (but so many smart birds)?”****by Karin Isler and Carel P. van Schaik****Contents**

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Material and methods**Overview**

Data on fertility rates (total number of offspring produced per year), age of first reproduction (age at first conception) and maximum lifespan (both from field data or in captivity) were collected from the literature. From these data, r_{\max} was obtained by solving Cole's (1954) equation numerically (using Mathematica 5.0.1). Brain and body mass data was taken from our large compilation. In total, data on 536 eutherian mammals and 399 avian species have been compiled, but 11 bird species were excluded from analyses due to very low values of recorded maximum lifespan compared to congeneric species. All variables were \log_e transformed before analysis, and statistical tests were parametric, using JMP 5.0.2. As we are mainly interested in the significance of a relationship rather than in the value of the slope of the regression line, least-squares regressions were applied, although major axis regressions would give more appropriate estimations of the slope of the lines in interspecific datasets (Martin & Barbour, 1989).

In mammals, species were defined as precocial if the young open their eyes at birth or shortly thereafter. Most families of Chiroptera produce one single, large offspring after a long gestation, but this opens its eyes only after some days. Thus, all Chiroptera are omitted in the analyses where the data are split by development mode, but included in the analysis of the combined dataset. In birds, development modes were defined according to Ricklefs and Starck (1998): altricials, semi-altricials, semi-precocials and precocials.

To control for the effects of phylogenetic relationships, the method of calculating independent contrasts was applied using the PDAP:PDTree package (Garland et al., 1992; Garland et al., 1993) of the Mesquite computer program (Maddison & Maddison, 2007). Polytomies in the phylogeny were resolved arbitrarily to branches with length zero. Although this results in a slight overestimation of type I error rates (Purvis & Garland, 1993), in practice differences to the algorithm used in CAIC (Purvis & Rambaut, 1995) are negligible if the number of species in the tree is large. The regression lines were constrained to pass through the origin (Garland et al., 1992).

To analyse the distribution of relatively large-brained taxa across mammals and birds, residuals from a least-squares regression of brain mass vs. body mass were calculated. Discrete data were obtained by grouping these residuals according to percentiles. Then, retention indices of relative brain size of both mammals and birds were calculated in MacClade 4.07 (Maddison & Maddison, 2005).

Mammals:

Data:

We compiled a broad data set on average brain and body mass as well as annual fertility, age at reproductive maturity and maximum lifespan of eutherian mammals (1248 species). Life history data was taken from published compilations (Egoscue et al., 1970; Sacher & Staffeldt, 1974; Kingdon, 1977; Mace & Eisenberg, 1982; Swihart, 1984; Gittleman, 1986b; Lee et al., 1991; Hayssen et al., 1993; Silva & Downing, 1995; Nowak, 1999; Ross & Jones, 1999; Carey & Judge, 2000; Miller et al., 2002; Ernest, 2003; Wiese & Willis, 2004; Weigl, 2005). If data from several populations or subspecies was available, the median value was used as a species mean. In contrast to Ernest (2003), data sources were not pooled, as this can lead to inadvertent duplication of source values. Reaching adulthood was defined as the age at which first conception took place (age at first reproduction minus gestation length) and was taken for females only, if available. Brain size measurements were also compiled from various sources (Oboussier & Schliemann, 1966; Pirlot & Stephan,

1970; Mace et al., 1981; Stephan et al., 1981; Mace & Eisenberg, 1982; Hafner & Hafner, 1984; Bauchot, 1985; Pirlot & Kamiya, 1985; Gittleman, 1986a; Bernard & Nurton, 1993; Iwaniuk et al., 2001; Hutcheon et al., 2002; Mann & Towe, 2003; Isler et al., in press and G. Mace pers. comm.). They all came from fully adult skulls and represent the mean of male and female values. Both brain mass and cranial capacity have been used as measures of brain size. When brain size was expressed in volume, these values were multiplied by 1.036 g/ml (the density of fresh brain tissue, Stephan, 1960; in Rehkamper et al., 1991) to obtain brain mass estimates.

Phylogeny:

Taxonomy follows Groves (2005) for primates and Nowak (1999) for all other mammals. Phylogenetic relationships are those proposed by Bininda-Emonds et al. (2007), including branch lengths estimations.

Birds:

Data:

Data were assembled from the literature, building on a large dataset of bird brain masses compiled mainly by Mlikovsky (1989a; 1989b; 1989c; 1990) and Iwaniuk & Nelson (2003), together with species mean body mass given in these sources (1748 species). All brain weight measurements came from fully adult skulls. Values represent the mean of male and female weights (see Iwaniuk & Nelson, 2002). Both brain weight and brain volume have been used as measures of brain size. Although brain mass is most often used, volumetric measures are considered equally valid because bird brains almost completely fill the cavum cranii (Mlikovsky, 1989a) and comparisons between volumetric values and brain weights found no significant differences (Iwaniuk & Nelson, 2001; Iwaniuk & Nelson, 2002).

Life history data (age at first reproduction, maximum lifespan and annual fertility rate) was compiled from several sources (mainly Schönwetter, 1960-1978; del Hoyo et al., 1992-2004). Complete information was available for 399 species, but 11 species were excluded due to unlikely low estimates of maximum lifespan compared to congeneric species.

Phylogeny:

Taxonomy followed Sibley and Monroe (1990). Phylogenetic relationships are those proposed by Katie Davis and Rod Page, University of Glasgow (Davis, 2008). The bird supertree is based on a strict consensus of 2000 trees run in Paup and assembles information from 748 published phylogenetic trees (Davis, 2008). The

phylogeny and further details are available online (Bird Supertree Project, <http://linnaeus.zoology.gla.ac.uk/~rpage/birdsupertree/>). For 1541 species, both brain mass data and phylogenetic information was available. The analysis of the distribution of residuals of brain vs. body mass for bird families is based on this reduced dataset. Family averages were calculated from species means. For calculating the retention index, MacClade allows a maximum number of 1500 taxa. Thus, 41 taxa were omitted arbitrarily.

Because branch length was unavailable, we set all branch lengths equal to 1.0. Sensitivity analysis branch carried out by running all the analyses using three arbitrary methods (Grafen's, Pagel's and Nealen's method as described in Garland et al., 1999), demonstrated that the results did not depend upon which branch lengths were used. Consequently, we present the results based on branch lengths equal to 1.0, which was justified (absolute contrasts vs. square root of the sum of branch lengths: slopes not significantly different from zero for all variables, Garland et al., 1999).

As this supertree contains some ambiguities (Davis, 2008), we repeated all analyses also with a supertree based on Sibley and Ahlquist's DNA-DNA hybridisation data (Sibley et al., 1988), as well as on more recent molecular studies (Sheldon et al., 1992; Sheldon & Winkler, 1993; Livezey, 1995; Livezey, 1996; Bleiweiss et al., 1997; Cohen et al., 1997; Cibois & Pasquet, 1999; Cibois et al., 1999; Crochet et al., 2000; DeFilippis & Moore, 2000; Dimcheff et al., 2002; Donne-Goussé et al., 2002; Yuri & Mindell, 2002; Irestedt et al., 2004), also using equal branch lengths. However, the results did not differ from those of the Davis tree in their level of significance.

Bivariate least-squares regressions of r_{\max} on brain mass and body mass

Table A1: Bivariate least-squares regressions of r_{\max} in mammals and birds (ln r_{\max} as dependent variable, ln body mass or ln brain mass as independent variable). The higher correlation coefficient r^2 is shown in bold face.

			Brain mass			Body mass		
	method	N	r^2	p	slope	r^2	p	slope
Mammals								
All species	raw	536	0.563	<0.0001	-0.447	0.485	<0.0001	-0.310
	IC	535	0.129	<0.0001	-0.349	0.094	<0.0001	-0.200
Altricials	raw	249	0.596	<0.0001	-0.488	0.584	<0.0001	-0.367
	IC	248	0.115	<0.0001	-0.366	0.099	<0.0001	-0.213
Precocials	raw	256	0.439	<0.0001	-0.398	0.244	<0.0001	-0.198
	IC	255	0.151	<0.0001	-0.344	0.078	<0.0001	-0.177
Terrestrial								
Carnivora	raw	98	0.477	<0.0001	-0.439	0.472	<0.0001	-0.286
	IC	97	0.253	<0.0001	-0.418	0.150	<0.0001	-0.226
Non-canid								
Carnivora	raw	79	0.654	<0.0001	-0.495	0.581	<0.0001	-0.303
	IC	78	0.337	<0.0001	-0.468	0.169	<0.0001	-0.229
Birds								
All species	raw	388	0.350	<0.0001	-0.364	0.308	<0.0001	-0.199
	IC	387	0.102	<0.0001	-0.321	0.129	<0.0001	-0.213
Altricials	raw	137	0.461	<0.0001	-0.330	0.527	<0.0001	-0.233
	IC	136	0.118	<0.0001	-0.209	0.114	<0.0001	-0.143
Semi-altricials	raw	77	0.590	<0.0001	-0.671	0.669	<0.0001	-0.398
	IC	76	0.157	<0.0001	-0.587	0.329	<0.0001	-0.400
Semi-precocials	raw	42	0.075	0.079	-0.208	0.027	0.302	-0.082
	IC	41	0.115	0.069	-0.227	0.034	0.266	-0.095
Precocials	raw	132	0.183	<0.0001	-0.241	0.121	<0.0001	-0.114
	IC	131	0.145	<0.0001	-0.366	0.070	<0.0001	-0.171

Are our results a statistical artefact?

The fact that the correlations for brain mass are generally stronger than for body mass may simply be because brain mass is actually a more accurate indicator of size than is body mass. Sacher (1959) found that lifespan is more closely correlated with brain mass than with body mass. Economos (1980), however, showed that this is also true for other internal organs such as the liver, suggesting that the stronger correlation between life histories and brain mass is due to the relatively great intra-specific variance in body mass rather than to any special link between life histories and the brain. Have we fallen into the same trap as, purportedly, Sacher (see also Harvey & Krebs, 1990)? Body mass is notoriously variable within species, and less variable organs (such as the brain) seem to provide a more reliable measure of size.

Unfortunately, this problem is not solved by the use of multiple regression. Still, it would be most unlikely that the observed patterns of correlation vary between groups of taxa exactly in the way predicted by the Expensive Brain framework, if the results were indeed due to a statistical artefact. For instance, why should brain mass not be a better predictor of body size in altricial birds, too? But a much stronger test is possible. If our results are indeed based on an artefact, the same general pattern should be found for other organs, such as the liver, the heart or muscle mass, which also tend to vary much less than body mass and may thus be a better estimate of actual body size. If, on the other hand, the r_{\max} -brain size correlation is biologically meaningful, other organ masses should not be negatively correlated with r_{\max} .

We have conducted analogous analyses using other organ masses instead of brain mass to predict r_{\max} . Data for mammals are taken from Crile & Quiring (1940), and pectoral muscle mass data for birds are taken from Magnan (1922) as listed in Viscor & Fuster (1987).

The results presented in Table A2 are fully consistent with our predictions. In mammals, only brain mass is significantly correlated with r_{\max} , whereas none of the other organs show any significant correlation at all. The results also hold if precocials and altricials are analyzed separately, although not always yielding significant results due to the smaller sample sizes.

In birds, the situation is more complex. We lack data on organ weights for a sufficiently large number of species. However, there are data on pectoral muscle mass, and we could show (Isler and van Schaik 2006) that there is a trade-off in the maintenance category in birds: species with relatively large brains have relatively small pectoral muscles and vice versa (probably due to the high energetic demands of flight). Thus, we would expect that in precocial birds, r_{\max} and pectoral muscle mass will be correlated through an indirect effect of brain mass on both variables.

Table A2: Multiple least-squares regressions of r_{\max} vs. various organ masses in mammals and birds (ln r_{\max} as dependent variable, ln body mass and, subsequently, ln of each organ mass as independent variables). For both body mass and organ mass, p-values and the correlation coefficient with r_{\max} are listed. As the observed correlation between r_{\max} and brain mass differs completely between altricial and precocial birds, those two development modes are analysed separately in birds. Significant effects are shown in bold face.

	N	r^2	Body mass		Organ mass	
			p	estimate	p	estimate
Mammals						
Heart mass	88	0.58	0.013	-0.564	0.331	+0.219
Lung mass	83	0.567	0.064	-0.319	0.864	-0.028
Liver mass	83	0.626	0.015	-0.495	0.489	+0.152
Kidney mass	79	0.627	0.029	-0.385	0.887	+0.028
Brain mass	87	0.716	0.005	0.298	<0.0001	-0.944
Birds (precocial)						
Pectoral muscle mass	58	0.162	0.015	-0.523	0.069	+0.407
Brain mass (for the same sample)	57	0.243	0.188	+0.248	0.021	-0.753
Birds (altricial)						
Pectoral muscle mass	53	0.682	<0.0001	-0.711	0.002	+0.482
Brain mass (for the same sample)	52	0.621	0.057	-0.159	0.324	-0.122

This is, indeed, found in our sample, although the correlation is just shy of significance ($p=0.069$, Table A2). Relatively large-brained precocial birds exhibit a relatively low r_{\max} (and, at the same time, relatively small pectoral muscles). Thus, the (positive) correlation between r_{\max} and pectoral muscle does not arise because pectoral muscle mass is a better estimator of body size than body mass, but because of the energy trade-off between its size and that of the brain.

In altricial birds, on the other hand, as r_{\max} and brain mass are not correlated, we would only expect a significant effect of pectoral muscle mass on r_{\max} , if pectoral muscle mass is a better estimate of body size than body mass itself. In this case, the correlation between r_{\max} and pectoral muscle mass should be negative, while the effect of body mass on r_{\max} should disappear or become positive. However, we observe a significantly positive correlation between pectoral muscle mass and r_{\max} ,

and the negative effect of body mass on r_{\max} is maintained (Table A2). In other words, altricial bird species with relatively large pectoral muscles for their body mass exhibit an increased reproductive capacity as proxied by r_{\max} , independent of their brain size. It is beyond the scope of the present paper to interpret this interesting result, but regardless, in altricial birds as in precocial ones, pectoral muscle mass is not a better predictor of body size than body mass itself. Thus, we conclude that the relationships between brain size and r_{\max} obtained here are biologically meaningful and do not originate from a statistical artefact.

Which aspects of life history are associated with both brain size and r_{\max} ?

The maximum rate of population increase (also termed „intrinsic rate of natural increase“, e.g. Ross 1992), r_{\max} , is defined by Cole’s equation (21) in Cole (1954):

$$1 = e^{-r} + b(e^{-r \cdot \alpha} - e^{-r(\omega+1)})$$

with b = annual fecundity, α = minimum age at first reproduction (AFR) and ω = maximum age at last reproduction. Here, we use fertility (= $2 \cdot b$) and maximum lifespan as ω (except for humans, where $\omega = 45$ y (Hill & Hurtado 1996)).

Additionally, we define the maximum reproductive period (MaxRP) as max. lifespan minus AFR. Sample sizes are given in Table A3.

Table A3: Sample sizes (number of species).

Mammals		Birds	
Altricials	Precocials	Altricials	Precocials
249	256	142	127

Correlations between components of r_{\max}

All life history traits that contribute to r_{\max} are highly correlated with each other (after partialling out body mass), except maximum lifespan and fertility in altricial birds (Table A4). From the definition, we expect that fertility and maximum lifespan, as well as maximum reproductive period are positively correlated with r_{\max} , whereas age at first reproduction is negatively correlated with r_{\max} .

Table A4: Pairwise correlations between components of r_{\max} (AFR, max. lifespan and fertility), partialling out body mass.

	Altricials		Precocials	
	r	p	r	p
Mammals				
AFR – max lifespan	0.230	0.0003	0.789	<0.0001
AFR – fertility	-0.485	<0.0001	-0.772	<0.0001
Max lifespan – fertility	-0.287	<0.0001	-0.671	<0.0001
Birds				
AFR – max lifespan	0.190	0.024	0.325	0.0002
AFR – fertility	-0.490	<0.0001	-0.573	<0.0001
Max lifespan – fertility	-0.024	0.778	-0.407	<0.0001

In all groups the partial correlation between maximum lifespan and r_{\max} is weak as compared to the other two variables (Table A5). In altricial mammals, maximum lifespan is even significantly negatively correlated with r_{\max} . In all groups, MaxRP is not positively correlated with r_{\max} if fertility is partialled out (Table 2A in the main text). In precocial mammals, MaxRP is even significantly negatively correlated with r_{\max} .

Table A5: Partial correlations between r_{\max} and its components (AFR, max. lifespan and fertility), partialling out body mass and the other two life history variables.

	Altricials		Precocials	
	r	p	r	p
Mammals				
AFR	-0.975	<0.0001	-0.902	<0.0001
Max lifespan	-0.158	0.013	0.195	0.002
Fertility	0.931	<0.0001	0.948	<0.0001
Birds				
AFR	-0.982	<0.0001	-0.994	<0.0001
Max lifespan	0.191	0.025	0.037	0.682
Fertility	0.987	<0.0001	0.993	<0.0001

Correlations between brain mass and components of r_{\max}

Life history traits that contribute to r_{\max} are mostly correlated with brain mass (even when body mass is partialled out), but not in altricial birds (Table A6). Note that, as a weak trend, fertility is even positively correlated with brain mass in the latter group. AFR is not correlated with brain mass in altricial mammals (cf. Isler & van Schaik, in review: The lengths of development periods are not correlated with brain size in altricial mammals).

Table A6: Pairwise correlation coefficients between brain mass and components of r_{\max} (AFR, max lifespan and fertility), partialling out body mass.

	Altricials		Precocials	
	r	p	r	p
Mammals				
AFR	0.092	0.147	0.650	<0.0001
Max lifespan	0.326	<0.0001	0.517	<0.0001
Fertility	-0.238	0.0002	-0.698	0.0002
Birds				
AFR	0.103	0.224	0.393	<0.0001
Max lifespan	0.076	0.372	0.341	<0.0001
Fertility	0.121	0.154	-0.324	0.0002

If not only body mass, but all life history variables are partialled out simultaneously, in each precocial group a different variable is no longer significantly correlated with brain mass (Table A7, next page): maximum lifespan in precocial mammals, fertility in precocial birds. To clarify the patterns, we look at partial correlations between MaxRP, fertility and brain mass (as usual also partialling out body mass). Table 2B in the main text shows that fertility rate is negatively correlated with brain mass in three groups (all except altricial birds), while MaxRP is positively correlated with brain mass only in altricial mammals and precocial birds.

Conclusion

In both altricial and precocial mammals, as well as in precocial birds, the negative correlation between r_{\max} and brain size can mostly be attributed to the influence of fertility rate. The absence of a correlation in altricial birds can also be attributed to fertility rate, which is not negatively, but even positively correlated with brain mass (controlling for body mass, as a weak trend).

Table A7: Partial correlation coefficients between brain mass and components of r_{\max} (AFR, Max lifespan and fertility), partialling out body mass and the other two life history variables.

	Altricials		Precocials	
	r	p	r	p
Mammals				
AFR	-0.060	0.349	0.230	0.0002
Max lifespan	0.281	<0.0001	-0.035	0.580
Fertility	-0.169	0.008	-0.405	<0.0001
Birds				
AFR	0.139	0.103	0.247	0.006
Max lifespan	0.052	0.546	0.219	0.015
Fertility	0.162	0.058	-0.066	0.464

Distribution of large-brained taxa in mammals and birds: retention indices

Table A8: Retention indices (RI) for relatively large brain size in mammals (N=1231) and birds (N=1500). Groups are based on percentiles of residuals of least-squares regressions of brain mass vs. body mass.

	Upper 10% of residuals		Upper 15% of residuals	
	Steps	RI	Steps	RI
Mammals	38	0.70	54	0.71
Birds	59	0.61	85	0.63

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