Revealing Multidimensional Associations in Life History Traits Across Four Animal Taxa

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Abstract

Trade-offs—negative associations among life history traits—are fundamental to understanding life history evolution. While traditional studies have focused mainly on pairwise trait relationships, organisms allocate finite energy across multiple processes simultaneously, necessitating a multivariate perspective. Here, by integrating both bivariate and multivariate phylogenetic frameworks, we investigated the complex relationships among six key life history traits (adult body size, offspring size, development time, adult lifespan, clutch size, and clutch frequency) across species of mammals, birds, reptiles, and insects. We demonstrated that multivariate frameworks significantly alter inferred trait relationships across species. For instance, a direct relationship between offspring size and adult lifespan becomes indirect when additional traits are considered. Moreover, while some multivariate patterns are consistent across taxa, others are taxon-specific. Our findings suggest that life history variations emerge from the interplay of multiple traits, emphasizing the need to view life history evolution through the lens of interconnected ecological and evolutionary processes.

Keywords: life history, trade-off, multivariate correlation, phylogenetic comparative method, phylogenetic path analysis

Introduction

Life history traits are measurable characteristics of an organism that determine its survival, growth, and reproductive success, such as body size, developmental duration and overall lifespan. These traits vary substantially across taxa, reflecting the diverse strategies used by different taxa in response to varying evolutionary pressures[1–4]. For example, mammals and birds typically exhibit lower reproductive rates and higher levels of parental investment, enhancing offspring survival in relatively stable environments. In contrast, fish and amphibians tend to have higher reproductive rates and shorter growth periods, strategies that maximize reproductive output and population survival in unstable environments[1–4].

Researchers have developed life history theory as a conceptual framework to explain the evolution of distinct life history strategies adopted by different organisms. Central to this framework is the idea of life history trade-offs, which arise because organisms have limited energy, time and nutrient that must be allocated among competing functions such as growth, reproduction, and maintenance[5–7]. Consequently, increased investment in one function necessarily reduces the resources available for another, leading to trade-offs among life history traits[5–7]. For instance, the trade-off between survival and reproduction is evident in organisms like annual herbs and insects, which allocate more resources to reproduction at the cost of their long-time survival, ensuring reproductive success in environments with high mortality risks[4,8,9].

Although numerous empirical studies have provided evidence for theoretical trade-offs among life history traits, examples have also been identified that do not conform to theoretical expectations. For example, the expected trade-off between body size and clutch size is sometimes absent or even reversed in amphibians or reptiles, where larger individuals may achieve higher reproductive outputs simultaneously[3,10]. Moreover, the relationship between specific life history traits can vary across taxa. For example, a negative correlation between development and reproduction has been consistently

observed in mammals and birds[2,3], yet this relationship was not always found in certain plants and insects[9,11].

Why was the evidence on the life history trade-offs mixed? One potential reason is that most of the current studies have only examined bivariate correlations between pairs of life history traits, while overlooking the possible multivariate relationships among these traits[12,13]. For instance, in *Drosophila*, the challenge of ephemeral food resources can simultaneously enhance stress resistance, metabolic reserves, and somatic maintenance at the expense of reduced fecundity. Additionally, abundant feeding and breeding opportunities can favour increased larval competitive ability and high fecundity at the cost of reduced size and maintenance[14,15]. Such complex multidimensional trade-offs could arise because organisms have a finite energy budget that must be divided among multiple life history processes simultaneously, rather than just two traits at a time[16–18]. Consequently, correlations between pairwise traits can be obscured by additional traits, leading to discrepancies between theoretical predictions and empirical findings[12,13,19].

To address these discrepancies, we carried out phylogenetic comparative analyses to investigate the relationships among six key life history traits, including adult body size (BS), offspring size (CS), development time (DT), adult lifespan (AL), clutch size (CS) and clutch frequency (CF) across a diverse range of animal species. Our work focused on two central questions: (1) Do multivariate relationships among life history traits alter the bivariate relationships observed between pairs of traits? (2) Are these multivariate relationships consistent across major animal taxa, including mammals, birds, reptiles, and insects? To answer these questions, we first used phylogenetic generalized least squares (PGLS) to investigate bivariate relationships between pairs of traits across species while accounting for phylogenetic relatedness. Next, we applied phylogenetic path analysis (PPA) to test multiple hypotheses regarding the multivariate relationships among these traits and identify the best-supported model (see Methods, Figure 1). By

comparing PGLS and PPA results, we differentiated direct pairwise associations from indirect associations mediated by other traits, providing deeper insights into the evolution of life history strategies in animals.

Methods

Data collection

(1) Life history traits

We collected species-level life history traits data from two key literature sources[4,20], which aggregated data from numerous studies on four major animal taxa: mammals[2,3,21], birds[2,3,22,23], reptiles[3,10], and insects[e.g., 24–26]. To enable cross-taxon comparisons, we focused on six key traits that are consistently available for all four animal taxa: (1) Adult body size: measured as adult body mass for vertebrate species, and body length for insects; (2) Offspring size: defined as offspring body mass for vertebrate species and body length for insect species; (3) Development time: measured as the time from birth to sexual maturity for vertebrates, and from hatching to adult eclosion for insects; (4) Adult lifespan: defined as the time from sexual maturity to death for vertebrates, and from adult eclosion to death for insects; (5) Clutch size: defined as the number of eggs per clutch or litter across all species, and (6) Clutch frequency: measured as the number of clutches or litters per year for vertebrate species, and per day for insect species, reflecting their typically shorter lifespan. Due to the absence of direct clutch frequency data for insect species, we estimated it indirectly via dividing the reported lifetime fecundity by clutch size, ensuring consistency across datasets.

For vertebrate taxa (i.e., mammals, birds and reptiles), we included only species with complete data for all six life history traits, resulting in a final dataset comprising 335 mammalian, 148 avian, and 417 reptilian species (Table S1). In contrast, for insect, restricting the dataset to only include insect species with complete data for all six traits would result in a small, taxonomically unrepresentative sample. To address this, we

applied a phylogenetic imputation method implemented in the R package *Rphylopars* (version 0.3.10) to impute the missing data while accounting for the phylogeny[27]. Specifically, we only included insect species with real data available for at least four of the six life history traits, and then imputed the remaining missing values. This approach resulted in a final dataset of 205 insect species, ensuring a complete and taxonomically representative insect dataset for subsequent analyses. Furthermore, all measurements of life history traits were natural log-transformed to meet the assumptions of statistical methods. The complete dataset used in this study is provided in supplementary material (Table S1).

(2) Phylogeny

We pruned published phylogenetic trees for each animal taxon to create phylogenies that reflect the shared evolutionary histories of the species included in our dataset. For mammals, we obtained the phylogenetic tree from Bakewell et al. [4], which was originally derived from Fritz et al. [28], and pruned it using "*keep.tip*" function from the R package "*ape*" (version 5.8) [29] to include only the species present in our dataset. For reptiles, Bakewell et al. [4] merged three existing molecular phylogenies[30–32], which we similarly pruned. The avian phylogeny used in this study was pruned based on a most recent avian molecular phylogeny inferring from genomic data[33]. For insects, the phylogeny used in this study was based on a most comprehensive insect molecular phylogeny available, which is constructed hierarchically using transcriptome, mitogenome data and species-rich DNA data[34]. The resulting phylogenetic trees for each taxon are provided as dendrograms in the supplementary material (Figure S1).

Statistical analyses

(1) Phylogenetic generalized least squares

We used phylogenetic generalized least squares (PGLS) [35] to examine the pairwise relationships between every pair of life history traits across species within each taxon. PGLS is a statistic approach that fits a linear model while accounting for the

phylogenetic non-independence among species, and can incorporate different evolutionary models (e.g., Pagel's λ, Brownian motion or early burst) to define the distribution of the residuals from the linear model[36]. We used Pagel's λ model in our main analyses. Pagel's λ, ranging from 0 to 1, measures the phylogenetic signal in the data: $\lambda = 0$ implies that the traits are independent of the phylogeny (i.e., there is no phylogenetic signal), whereas $\lambda = 1$ suggests that the traits perfectly follow the phylogenetic relationships as expected under a Brownian motion model of evolution[37]. We conducted PGLS using R package "*caper*" (version 1.0.3) [38], which estimates λ by automatically determining the value that maximizes the likelihood of the fit of the data to the phylogenetic tree and regression model, ensuring optimal branch length transformations given the dataset. For each PGLS model, we derived the regression coefficients and associated statistical outputs, including t-values, *P*-values, and R-squared (R^2) statistics to assess the significance, explanatory power of the regression and the overall fit of the models to the data (Table S2). We initiated our analysis to test all pairwise relationships (Figure 1) between life history traits in mammals. Then, we extended our investigation by conducting separate PGLS models to examine the correlations between life history traits across species within other taxa, including birds, reptiles and insects.

(2) Phylogenetic path analyses

We employed phylogenetic path analysis (PPA) [39,40] to examine the multivariate relationships, including both direct and indirect associations, among diverse life history traits across species. PPA is an extension of structural equation modelling (SEM) approach that can test the goodness-of-fit of the data to different hypotheses regarding the associations among multiple variables while incorporating phylogenetic regression methods, such as PGLS, to account for phylogenetic non-independence among species [41,42].

We carried out the PPA by testing previously proposed hypotheses. Previous studies

have documented several robust associations, including: positive associations between adult body size and offspring size or lifespan[2,8,43], and between adult body size, offspring size and development time[14,44,45]. Additionally, a trade-off between clutch size and offspring size or development time has been consistently reported[46–48]. In contrast, some associations remain contentious, with inconsistent findings in literature, such as those between body size and clutch size, and between development time and lifespan[2,4,49]. To simplify hypothesis testing, we first incorporated the well-established associations into all candidate models as fixed components (Figure 1, Table S3). Next, for the associations that remain debated or unresolved, we systematically included or excluded them across various candidate models, generating a list of distinct hypotheses for evaluation (Figure 1; Table S3).

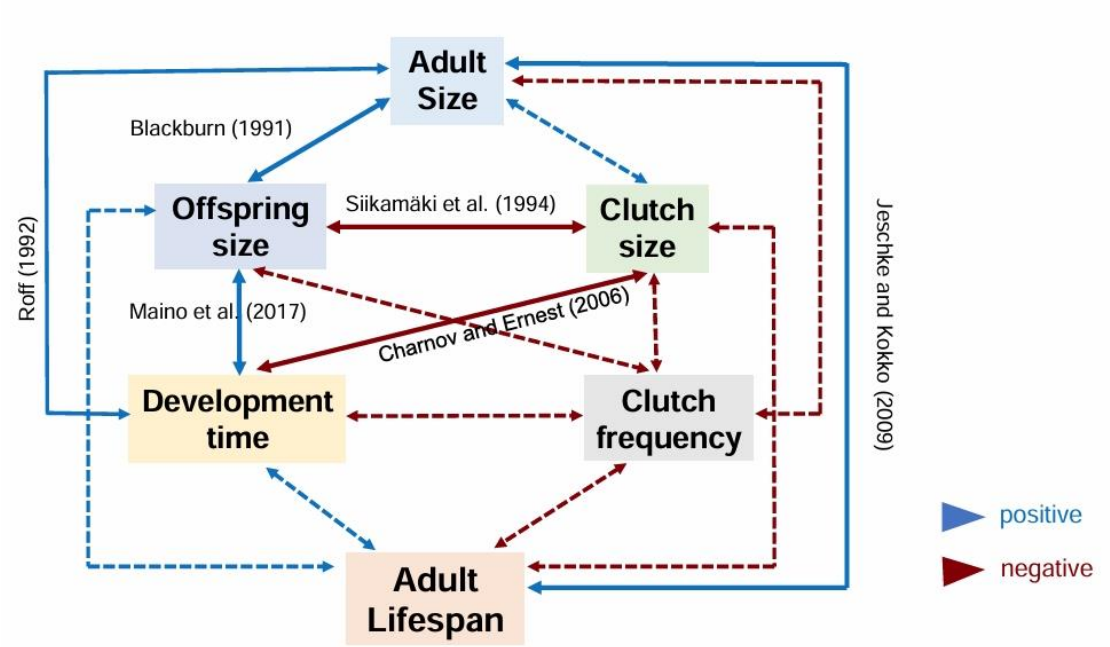

Figure 1. Conceptual diagram illustrating the hypotheses of our study, highlighting the hypothetical relationships among life history traits. Blue arrows indicate hypothesized positive direct associations between life history traits, while red arrows denote negative correlations. Solid lines represent well-established associations consistently supported by previous studies, and were therefore included in every candidate models in phylogenetic path analysis. In contrast, dotted lines denote associations that were not consistently observed, reflecting mixed support across different studies. References for the well-established associations are provided alongside the corresponding arrows.

We initially conducted PPA on mammalian life history traits utilizing the R package "*phylopath*" (version 1.3.0) [50] while assuming Pagel's λ model for the trait evolution. We tested the goodness-of-fit for a list of 511 candidate models, each represented as a formula in Tables S3. Model fitting was assessed via the Fisher's C statistic, with a proposed model deemed a good fit if the C statistic was non-significant ($P > 0.05$) [41,42]. Moreover, to rank the candidate models and identify the best-supported model, we calculated the C statistic information criterion (CICc) for each model[39,40], analogous to the Akaike information criterion (AIC). The best-supported model was the one with a non-significant C statistic ($P > 0.05$) and the lowest CICc value, when the difference in CICc (ΔCICc) between this model and the next best model did not exceed 2[42]. We then conducted PPA for the other animal taxa following the same protocol, enabling comparisons with the patterns observed in mammals.

Visualization

Phylogenetic relationships among species were visualized using dendrograms generated with the *ggtree* package (version 3.13.0.1) [51]. We mapped the life history trait values for each species onto the tips of the phylogenetic trees, with color gradients representing trait value variation. In addition, we created graphical representations of the relationships among multiple life history traits when reporting the results of PGLS models and PPA. All visualizations were produced in R (version 4.4.1) [52] using the *ggplot2* package (version 3.5.1) [53].

Sensitivity Analyses

We used different evolutionary models in phylogenetic imputation method, PGLS, and PPA to check whether our findings are robust to alternative evolutionary models. The alternative evolutionary models included Brownian motion (BM) and early burst (EB). The results of these sensitivity analyses are presented in supplementary materials (Figures S2-6 and Tables S2 and S5).

Results

PGLS revealed bivariate associations among life history traits in mammals.

We formulated hypotheses regarding the relationships among life history traits, drawing from previous studies (see in Methods, Figure 1). Using PGLS while assuming a Pagel's λ model, we tested these hypotheses by examining the bivariate associations between pairs of life history traits across species while accounting for phylogenetic non-independence (Figure 1). Our main analysis focused on mammals, compiling data on six key life history traits across 335 mammalian species: adult body size (BS), offspring size (OS), development time (DT), adult lifespan (AL), clutch size (CS), and clutch frequency (CF) (Figure 2a).

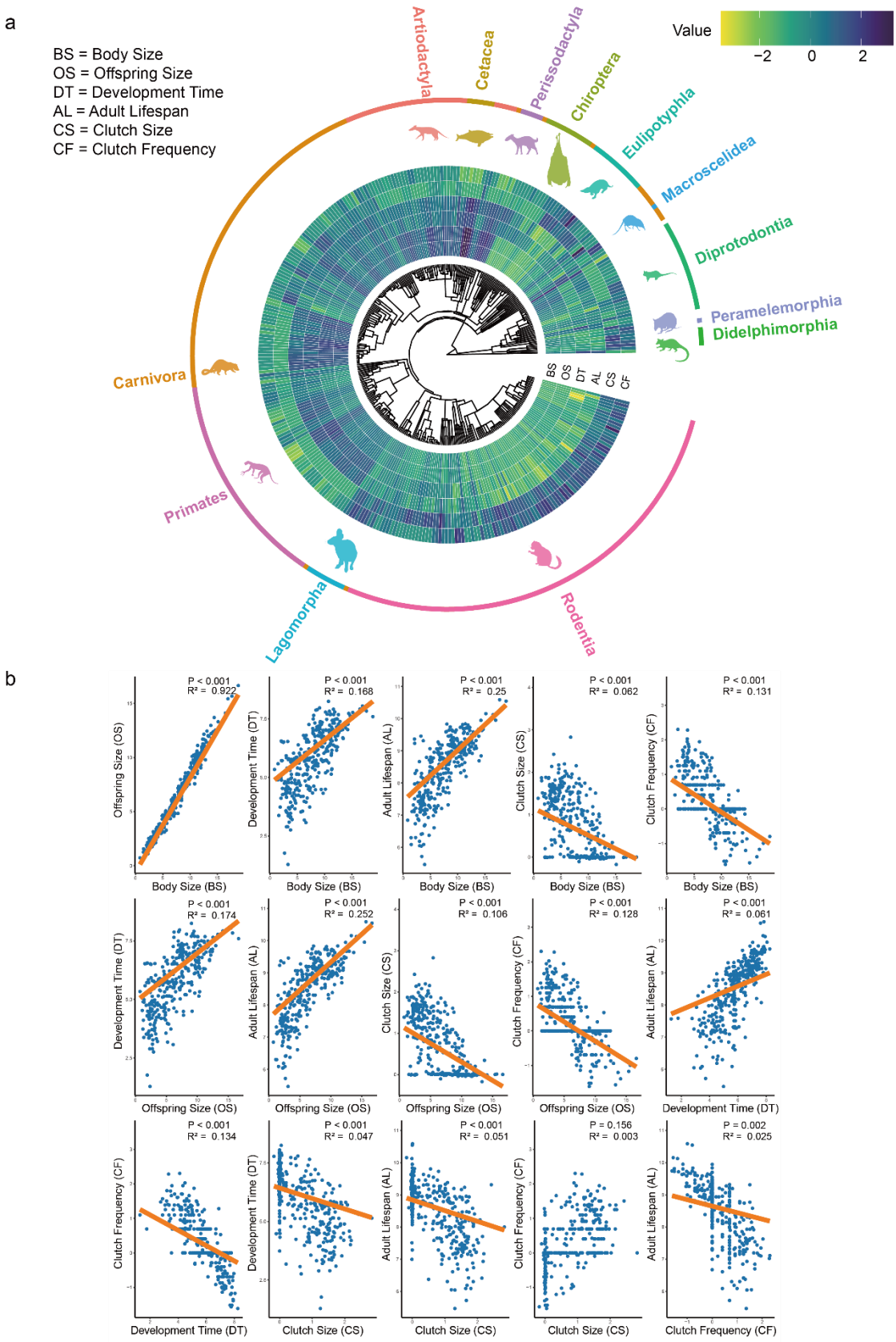

Figure 2. Phylogenetic correlations between life history traits in mammalian species. (a) Phylogenetic tree of 335 mammalian species, with heatmap rings displaying life history trait values.

Ring colours range from yellow (low value) to dark purple (high value). All measurements of life history traits were natural log-transformed and standardized. The outermost rings denote the major mammalian orders. Strong covariation is observed among life history traits across species, for example, between body size, offspring size, development time and lifespan. (b) The correlations among pairs of life history traits across 335 mammalian species derived from PGLS models. Each dot represents a species, with its coordinates corresponding to the values of two life history traits. The best-fit regression line represents the overall trend.

First, we validated all previously well-established associations (Figure 1). Specifically, we confirmed the positive correlations between adult body size and both offspring size and lifespan (PGLS, OS ~ BS, $\beta \pm SE = 0.87 \pm 0.014$, $P < 0.001$; AL ~ BS, $\beta \pm SE = 0.158 \pm 0.015$, $P < 0.001$; Figure 2b; Tables 1 and S2). Additionally, we observed a positive correlation between adult size or offspring size and development time, while offspring size was negatively correlated with clutch size (PGLS, DT ~ BS, $\beta \pm SE = 0.186 \pm 0.022$, $P < 0.001$; DT ~ OS, $\beta \pm SE = 0.207 \pm 0.024$, $P < 0.001$; CS ~ OS, $\beta \pm SE = -0.089 \pm 0.014$, $P < 0.001$; Figure 2b; Tables 1 and S2). We also identified a significant negative association between clutch size and development time (PGLS, DT ~ CS, $\beta \pm SE = -0.448 \pm 0.107$, $P < 0.001$; Figure 2b; Tables 1 and S2). These findings are consistent with previously reported trends[2,8,14,45,46,48], reinforcing the robustness of these correlations in mammalian species (Figure 1).

Next, we examined associations that have received mixed support in previous studies (Figure 1). Our analysis confirmed some widely recognized associations among life history traits in mammals. Specifically, clutch frequency showed significant negative associations with adult body size, offspring size, development time, and lifespan (PGLS, CF ~ BS, $\beta \pm SE = -0.103 \pm 0.014$, $P < 0.001$; CF ~ OS, $\beta \pm SE = -0.112 \pm 0.016$, $P < 0.001$; CF ~ DT, $\beta \pm SE = -0.222 \pm 0.031$, $P < 0.001$; AL ~ CF, $\beta \pm SE = -0.202 \pm 0.065$, $P = 0.002$; Figure 2b; Tables 1 and S2). Additionally, we found lifespan had a positive correlation with offspring size or development time, as well as a negative association

with clutch size (PGLS, AL ~ OS, β ± SE = 0.174 ± 0.016, $P < 0.001$; AL ~ DT, β ± SE = 0.183 ± 0.038, $P < 0.001$; AL ~ CS, β ± SE = -0.333 ± 0.077, $P < 0.001$; Figure 2b; Tables 1 and S2). In contrast, we also revealed some correlations that deviated from existing hypothetical associations. While some studies have reported a positive relationship between adult body size and clutch size[3,10,54], our results indicated a trade-off between the two traits in mammals (PGLS, CS ~ BS, β ± SE = -0.063 ± 0.013, $P < 0.001$; Figure 2b; Tables 1 and S2). Finally, we found no significant correlation between clutch size and clutch frequency (PGLS, $P = 0.156$; Figure 2b; Tables 1 and S2).

Discrepancies between PGLS and PPA indicated indirect associations among life history traits.

We observed inconsistencies between the results of PGLS and the hypothetical associations or previous findings, which we attribute to a key limitation in earlier studies: Prior studies primarily focused only on pairwise relationships between life history traits, often overlooking the complex multivariate associations among multiple traits. In our dataset, we observed that life history traits such as body size, offspring size, development time and lifespan might strongly covary, suggesting that some observed pairwise correlations may result from confounding effects of additional variables (Figure 2a). Therefore, to examine whether multivariate associations would change the bivariate correlations, we used phylogenetic path analysis (PPA) to study life history evolution across 335 mammalian species, a method that simultaneously tests both direct and indirect relationships among traits while accounting for phylogenetic relationships[39,40].

We formulated 511 models to explore potential relationships among six life history traits, and conducted PPA to select the best-support model (Table S3, see Method for details). In the best-support model, we found that some direct correlations between pairs of traits were consistently observed in both PGLS and PPA models. Specifically, adult

body size showed positive direct correlations with offspring size, development time, and lifespan (PPA, OS ~ BS: β ± SE = 0.942 ± 0.015; DT ~ BS: β ± SE = 0.303 ± 0.191; AL ~ BS: β ± SE = 0.506 ± 0.062; Figure 3a; Table 1). Moreover, a significant positive direct correlation was also identified between between development time and both offspring size and lifespan (PPA, DT ~ OS: β ± SE = 0.169 ± 0.2; AL ~ DT: β ± SE = 0.08 ± 0.052; Figure 3a; Table 1). In contrast, a negative direct correlation was found between offspring size and clutch size (PPA, CS ~ OS: β ± SE = -0.721 ± 0.158; Figure 3a; Table 1). Both adult body size and development time were negatively associated with clutch frequency (PPA, CF ~ BS: β ± SE = -0.349 ± 0.068; CF ~ DT: β ± SE = -0.28 ± 0.055; Figure 3a; Table 1), Additionally, clutch size was negatively correlated to both development time and lifespan (PPA, DT ~ CS: β ± SE = -0.128 ± 0.058; AL ~ CS: β ± SE = -0.113 ± 0.052; Figure 3a; Table 1). We found no direct correlations between clutch size and clutch frequency in both PGLS models and PPA models (PPA, β = 0; Figure 3a; Table 1).

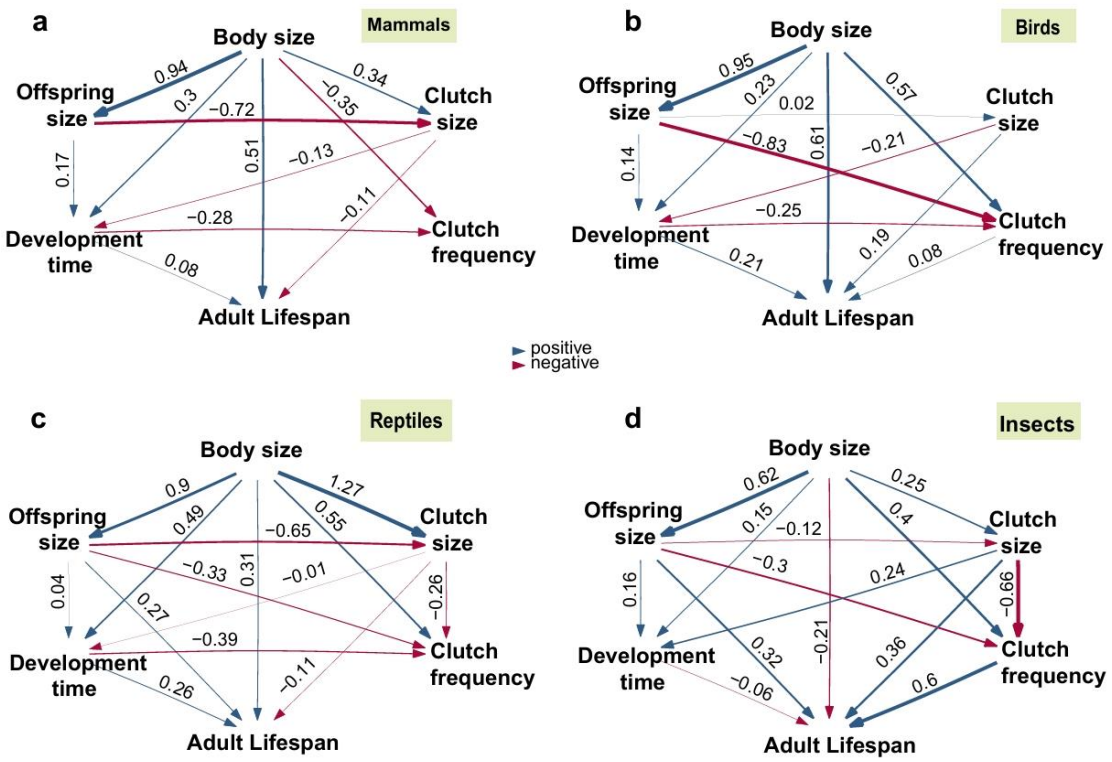

Figure 3. Best-supported models in phylogenetic path analysis using Pagel's λ model for (a) mammals, (b) birds, (c) reptiles and (d) insects. Blue arrows represent positive correlations, while

red arrows represent negative correlations, with their width corresponding to the magnitude of the standardized regression coefficients. Exact coefficient values are provided alongside the arrows.

Notably, some correlations identified in PGLS were not retained as direct associations in PPA, but were instead mediated by third variables, making them indirect associations in PPA models (Figure 3a; Table 1). Specifically, the negative association between offspring size and clutch frequency identified in PGLS was mediated by adult body size and/or development time in PPA (Figure 3a; Table 1). Similarly, the negative correlation between clutch frequency and lifespan was mediated through adult body size and/or development time, and the positive association between offspring size and lifespan was mediated by adult body size, development time and/or clutch size (Figure 3a; Table 1).

Table 1. Comparison of PGLS and PPA results for pairs of life history traits in mammals. The first column lists the trait pairs, and shaded rows indicate associations that were found discrepancies between the two models.

Model	PGLS (Coef ± SE)	PPA (Coef ± SE)
Offspring Size ~ Body Size	0.87 ± 0.014*	0.942 ± 0.015
Development Time ~ Body Size	0.186 ± 0.022*	0.303 ± 0.191
Adult Lifespan ~ Body Size	0.158 ± 0.015*	0.506 ± 0.062
Clutch Size ~ Body Size	-0.063 ± 0.013*	0.337 ± 0.156
Clutch Frequency ~ Body Size	-0.103 ± 0.014*	-0.349 ± 0.068
Development Time ~ Offspring Size	0.207 ± 0.024*	0.169 ± 0.2
Adult Lifespan ~ Offspring Size	0.174 ± 0.016*	0
Clutch Size ~ Offspring Size	-0.089 ± 0.014*	-0.721 ± 0.158
Clutch Frequency ~ Offspring Size	-0.112 ± 0.016*	0
Adult Lifespan ~ Development Time	0.183 ± 0.038*	0.08 ± 0.052
Clutch Frequency ~ Development Time	-0.222 ± 0.031*	-0.28 ± 0.055
Development Time ~ Clutch Size	-0.448 ± 0.107*	-0.128 ± 0.058
Adult Lifespan ~ Clutch Size	-0.333 ± 0.077*	-0.113 ± 0.052
Clutch Frequency ~ Clutch Size	0.095 ± 0.067	0
Adult Lifespan ~ Clutch Frequency	-0.202 ± 0.065*	0

Lastly, PPA revealed a reversal in the direction of one correlation: the association

between adult body size and clutch size, which was negative in PGLS, became positive in PPA (PPA, CS ~ BS, $\beta \pm SE = 0.337 \pm 0.156$; Figure 3a; Table 1).

Patterns found in mammals were partially consistent in other animal taxa.

We then extended the analyses to other animal taxa, including reptiles, birds and insects, to understand whether the patterns observed in mammals were consistent across these groups.

In PGLS models, many associations were consistent across animal taxa, while some notable exceptions (Figures S2-4; Table S2). For example, adult body size was negatively correlated with clutch size in mammals (PGLS, CS ~ BS, $\beta \pm SE = -0.063 \pm 0.013$, $P < 0.001$; Figure 2b; Tables 1 and S2). In contrast, reptiles and insects exhibited a significant positive association between these traits, while no relationship was detected in birds (PGLS, reptiles: $\beta \pm SE = 0.242 \pm 0.018$, $P < 0.001$; Figure S3b; insects: $\beta \pm SE = 0.374 \pm 0.128$, $P = 0.004$; Figure S4b; birds: $P = 0.521$; Figure S2b; Table S2).

In PPA models, we first identified several consistent direct correlations between pairs of life history traits across different animal taxa (Figure 3). Specifically, adult body size was positively correlated with both offspring size and development time across all four groups, as well as between offspring size and development time (Figure 3; Table S5).

Despite these common trends, we observed taxon-specific variations. In mammals, birds, and reptiles, we consistently observed positive direct associations between body size and lifespan (Figures 3a-c; Table S5). However, insects exhibited the opposite trends, with negative correlations (Figure 3d; Table S5). Similarly, while both clutch size and clutch frequency were negatively correlated with development time in mammals, birds and reptiles (Figures 3a-c; Table S5), insects displayed a positive correlation between clutch size and development time, and no significant direct correlation between clutch frequency and development time (Figure 3d; Table S5).

In addition, while positive direct correlations between adult size and clutch size were evident in mammals, reptiles and insects (Figures 3a, 3c and 3d; Table S5), no significant direct correlation was found in birds (Figure 3b; Table S5). Similarly, except birds (Figure 3b; Table S5), a negative correlation was consistently identified between offspring size and clutch size across most taxa (Figures 3a, 3c and 3d; Table S5). Additionally, no direct association was identified between clutch size and clutch frequency in mammals and birds, nor between clutch frequency and lifespan in mammals and reptiles (Figure 3; Table S5).

Notably, some associations observed in mammals reversed in other taxa (Figure 3; Tables S5). For example, the correlation between clutch size and lifespan was negative in mammals and reptiles (Figures 3a and 3c; Table S5), but became positive in birds and insects (Figures 3b and 3d; Table S5).

Sensitive analyses

We evaluated the robustness of the PGLS and PPA models across four taxa using two alternative evolutionary models, including Brownian motion (BM) and early burst (EB). The results derived from different evolutionary models displayed only minimal differences (Figures S5 and S6; Tables S2 and S5). For example, in mammals, while model with Pagel's λ did not detect a significant relationship between clutch size and clutch frequency (PGLS, $P = 0.156$; Figure 2b; Table S2), a negative correlation was demonstrated in the PGLS models with both BM and EB (PGLS, CF ~ CS, $\beta \pm SE = 0.132 \pm 0.06$, $P = 0.029$; Table S2). Furthermore, in the PPA models, the Pagel's λ model showed positive direct associations between body size and clutch size (PPA, CS ~BS, $\beta \pm SE = 0.337 \pm 0.156$; Figure 3a; Table S5), as well as between development time and lifespan (PPA, AL ~ DT, $\beta \pm SE = 0.08 \pm 0.052$; Figure 3a; Table S5). However, no direct relationships were observed between these traits in the PPA models with both BM and EB (PPA, $\beta = 0$; Figures S5a and S6a; Tables S5).

Discussion

In this study, we investigated the species-wise relationships among six key life history traits (e.g., adult body size, development time, and clutch size) across mammals, birds, reptiles, and insects. Using phylogenetic generalized least squares (PGLS) and phylogenetic path analysis (PPA), we examined both bivariate and multivariate relationships among these traits, uncovered patterns that traditional bivariate approaches could not capture alone, providing deeper insights into the evolution of animal life histories.

Traditional studies typically rely on bivariate analyses to assess relationships among life history traits[5,14,55,56]. While informative, such analyses may overlook confounding effects from additional variables[12,13,19]. Although multivariate methods like principal component analysis (PCA) have been used to reduce dimensionality[57–60], they do not allow for hypotheses testing or the disentanglement of more nuanced relationships among traits[13]. By employing PPA, we extended beyond these limitations to disentangle both direct and indirect associations among traits under a hypothesis-testing framework. This allowed us to reveal patterns that bivariate analyses alone cannot capture. For instance, although previous work supported a trade-off between adult body size and clutch size in mammals[2–4], our PPA revealed a direct positive correlation between these traits (Figure 3a; Table 1). Similarly, while earlier studies proposed a negative association between offspring size and clutch frequency[2–4], we found no direct relationship between these traits (Figure 3a; Table 1).

More importantly, these findings provide novel insights into the complex nature of life history evolution, offering implications that extend beyond previous theories. Traditional theories have framed organisms along a continuum from "fast" to "slow" life histories[6,7,56]. "Fast" life histories, characterized by rapid growth, early reproduction, and short lifespans, are typically associated with unstable environments.

In contrast, "slow" life histories involve slower growth, delayed reproduction, and longer lifespans, often reflecting adaptation to more stable conditions[61,62]. While this framework has been instrumental in explaining life history variation among organisms, accumulating evidence suggested that life history strategies are more complex than the traditional "fast-slow" model implies[12,13,19]. As Stott et al. [13] argue, this framework oversimplifies the intricate dynamics of life history evolution, and fails to account for the full diversity of strategies that exist beyond this continuum. Our findings support this perspective by demonstrating that life history evolution is shaped by complex, multidimensional relationships rather than simple bivariate correlations. We showed that some associations, such as between adult body size and clutch size in mammals, was actually mediated by other traits, such as development time, underscoring the importance of accounting for additional mediating variables when examining life history evolution. (Figure 3a).

Additionally, studies have also uncovered the genetic architecture underlying the multidimensional nature of life history trade-offs[19]. Genes with pleiotropic effects influence multiple traits simultaneously by regulating interconnected gene networks. Often acting as key transcription factors or components of signaling pathways, these genes coordinate multiple processes like survival, growth, and fecundity[19]. For instance, In *Glanville fritillary* butterflies, the pleiotropic gene *Sdhd* modulates critical metabolic pathways that enhances adult flight performance and dispersal capacity while concurrently imposing costs such as reduced metabolic rate and delayed lavral growth[63].

Furthermore, we observed taxon-specific life history strategies across different animal taxa. For example, in vertebrates, there is a positive relationship between adult body size and lifespan, and a negative relationship between clutch size and development time, but insects exhibit the opposite patterns on both associations (Figure 3). Such differences likely arise from the distinctions in the environments in which these groups

inhabit. Mammals and birds, which often inhabit relative stable and predictable environments, tend to invest in fewer offspring with extensive parental care and longer developmental periods[5,6,64,65]. Larger organisms in these groups generally exhibit slower metabolic rates, reduced reproductive rates, and prolonged parental investment, all of which contribute to longer lifespans and more gradual life histories[64–66]. This strategy allows for greater resource allocation per offspring, enhancing survival rates in stable habitats[61,62,67]. In contrast , insects often inhabit unpredictable environments with fluctuating resource availability[66,68]. To cope with these conditions, they adopt a high-fecundity strategy, producing large clutch sizes at the expense of individual offspring quality[69–71]. This leads to a positive correlation between clutch size and development time, as larger clutches intensify larval competition, prolonging maturation[72,73]. Additionally, a trade-off emerges between adult body size and lifespan: while larger body size enhances resource acquisition, it also increases predation risk, resulting in a negative correlation between body size and lifespan[74,75].

Variations in life history trait patterns across animal taxa indicate that the associations among these traits may differ depending on the taxonomic scale[76]. For example, recent studies have also revealed a greater diversity of strategies adopted by different individuals within populations. This study also revealed that individual variation does not always align neatly along a slow–fast continuum[60]. When more individual-level data are available, future studies should investigate the multivariate relationships among traits within species and compare with patterns observed across species to better understand life history evolution across scales.

Conflict of interest declaration. The authors declare no competing interests.

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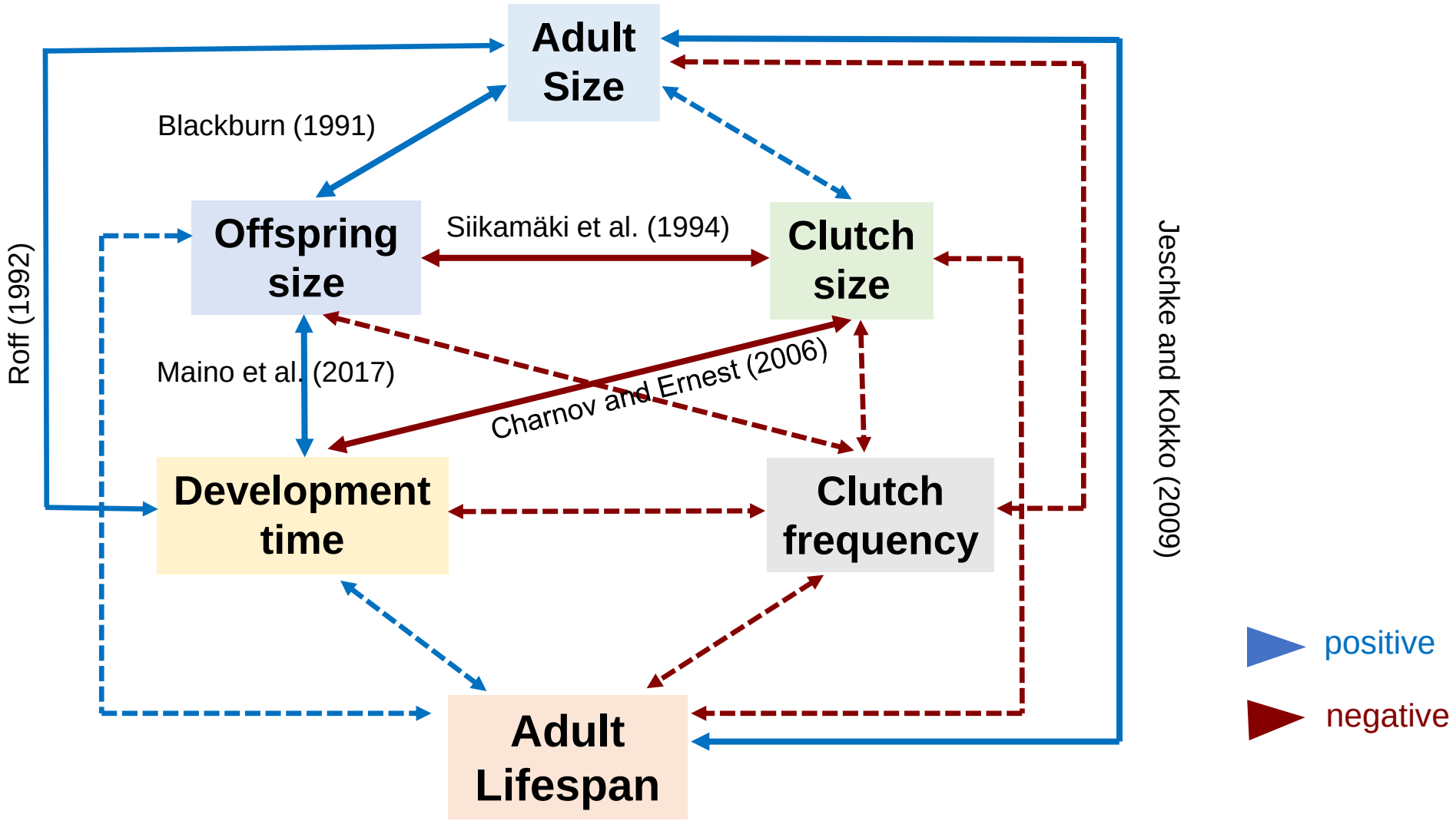
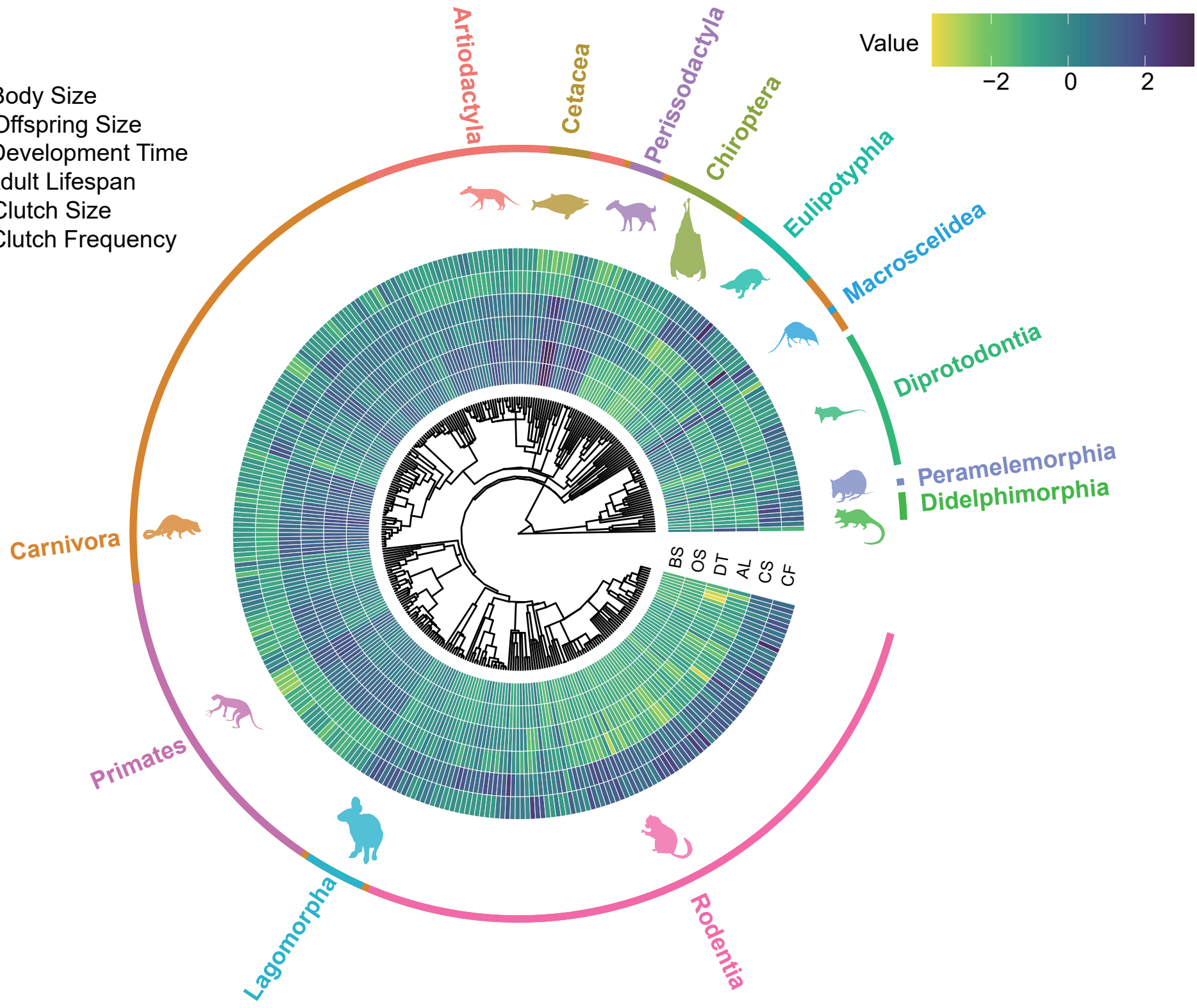
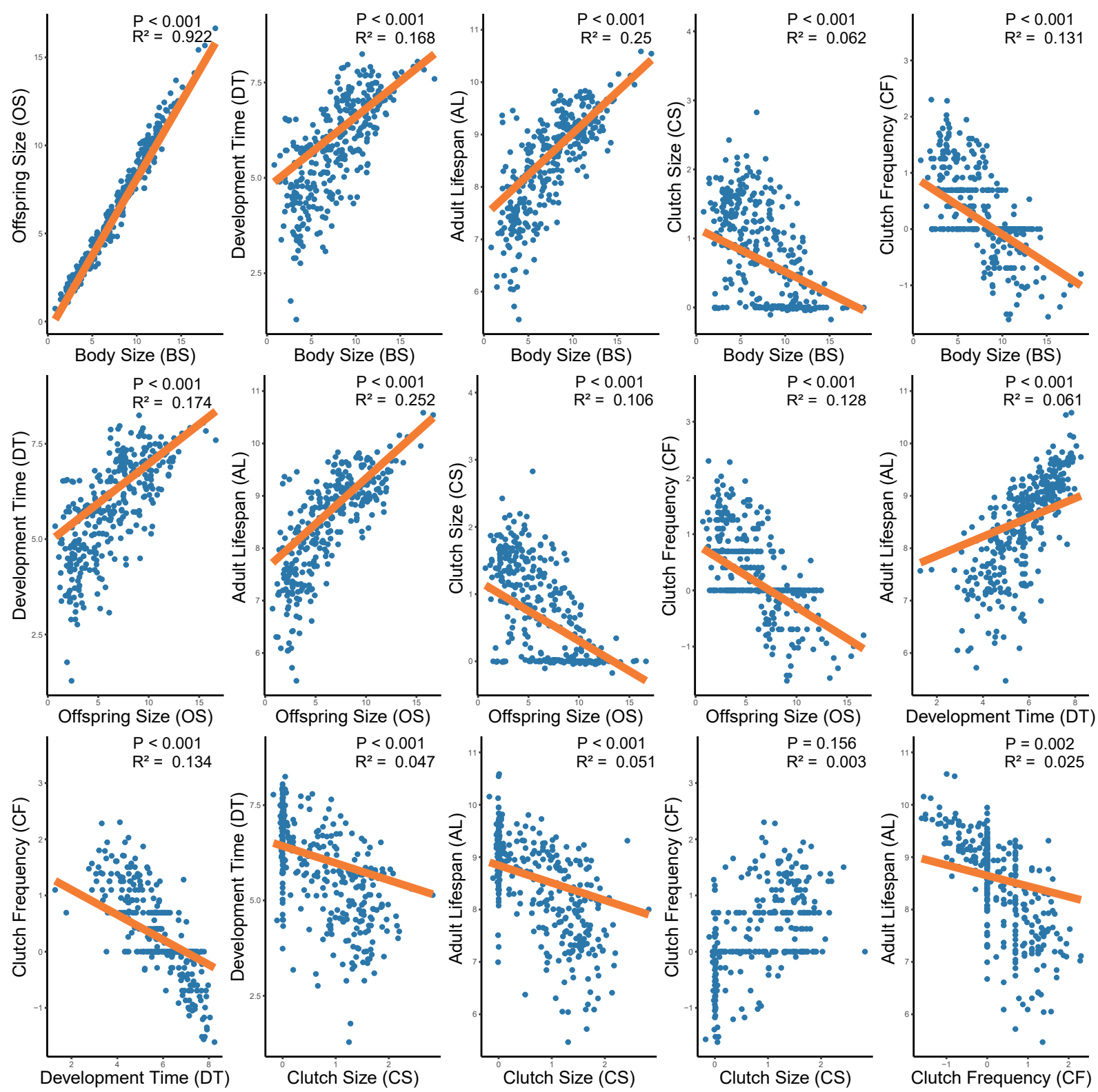

Adult Size
Blackburn (1991)
Offspring size
Siikamäki et al. (1994)
Clutch size
Roff (1992)
Maino et al. (2017)
Charnov and Ernest (2006)
Jeschke and Kokko (2009)
Development time
Clutch frequency
Adult Lifespan
positive
negative

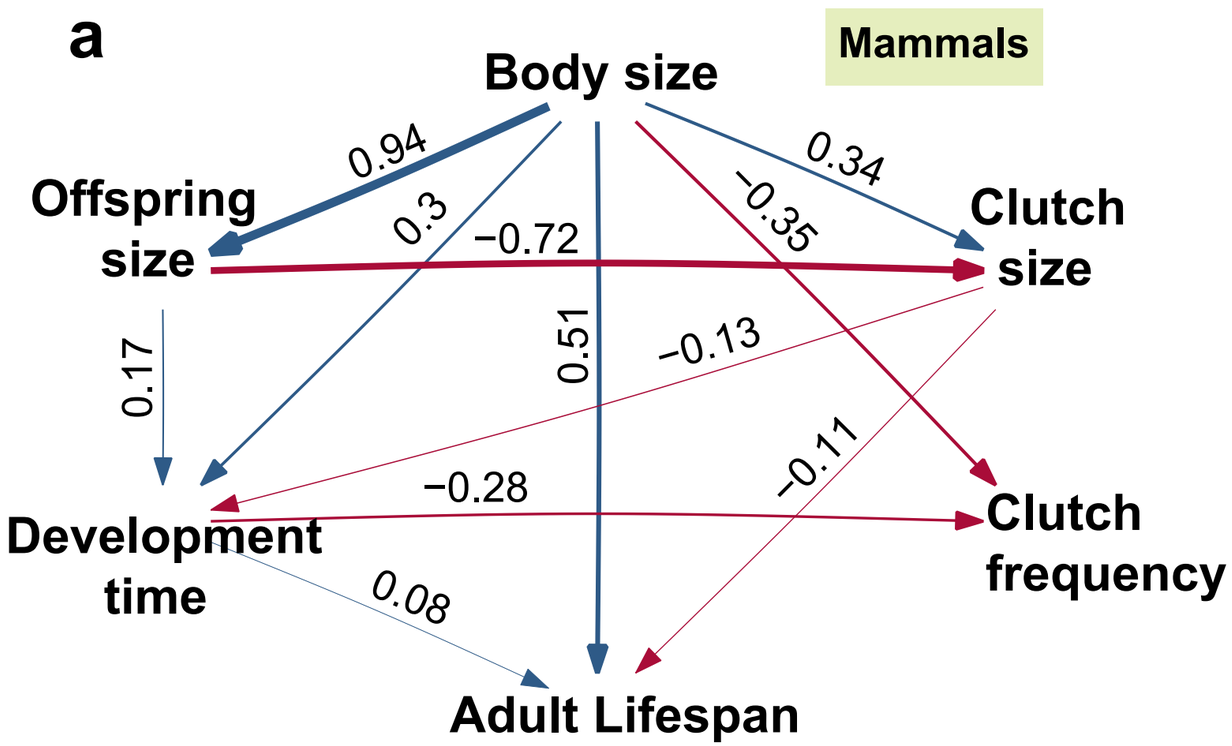
a

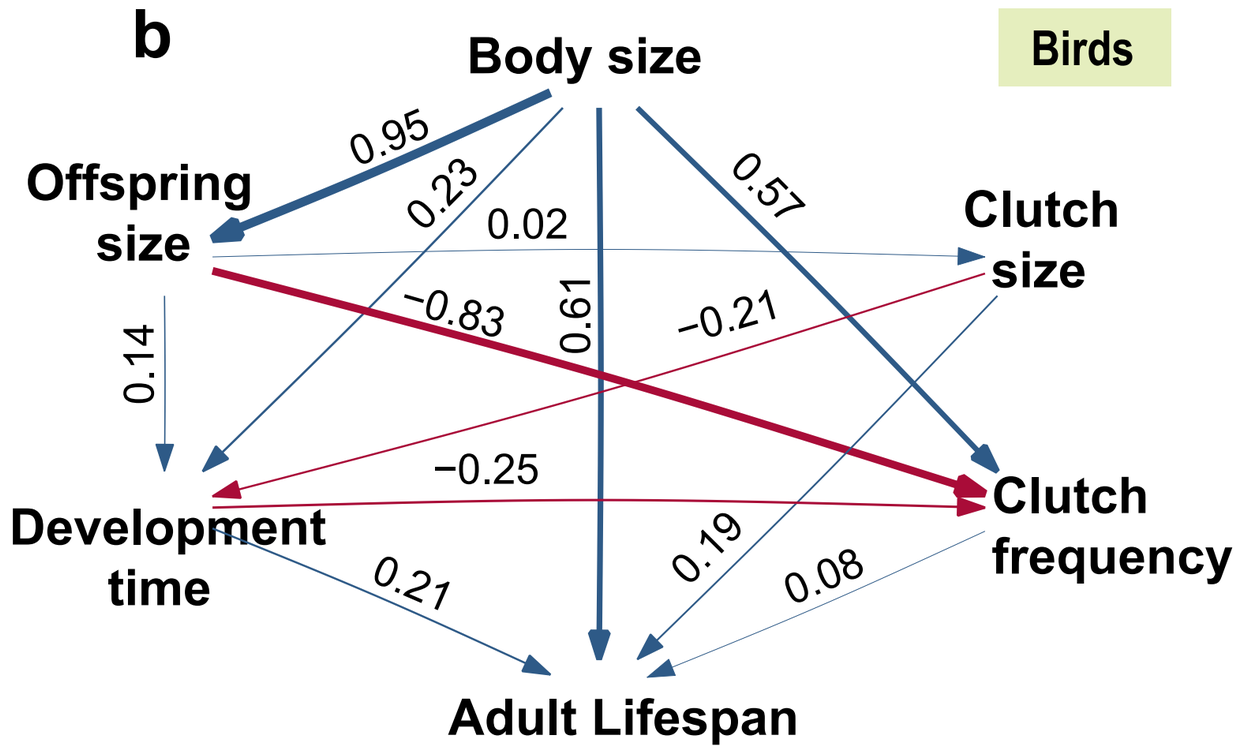
BS = Body Size
OS = Offspring Size
DT = Development Time
AL = Adult Lifespan
CS = Clutch Size
CF = Clutch Frequency



b




a
Mammals
Body size
Offspring size
Clutch size
Development time
Clutch frequency
Adult Lifespan
0.94
0.3
−0.72
0.34
−0.35
0.17
0.51
−0.13
−0.28
−0.11
0.08


b
Birds
Body size
Offspring size
Clutch size
Development time
Clutch frequency
Adult Lifespan
0.95
0.23
0.02
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0.14
−0.83
0.61
−0.21
−0.25
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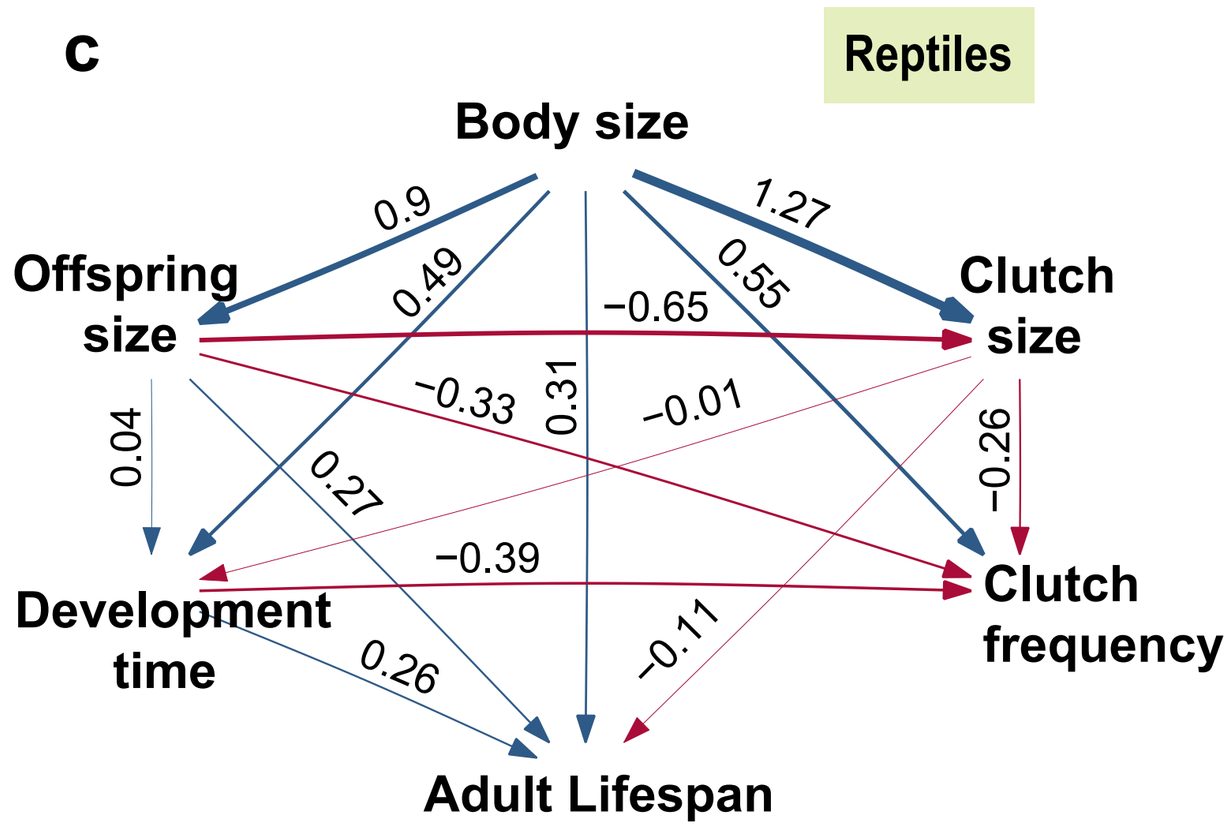
0.19
0.08

positive
negative


c
Reptiles
Body size
Offspring size
Clutch size
Development time
Clutch frequency
Adult Lifespan
0.9
0.49
−0.65
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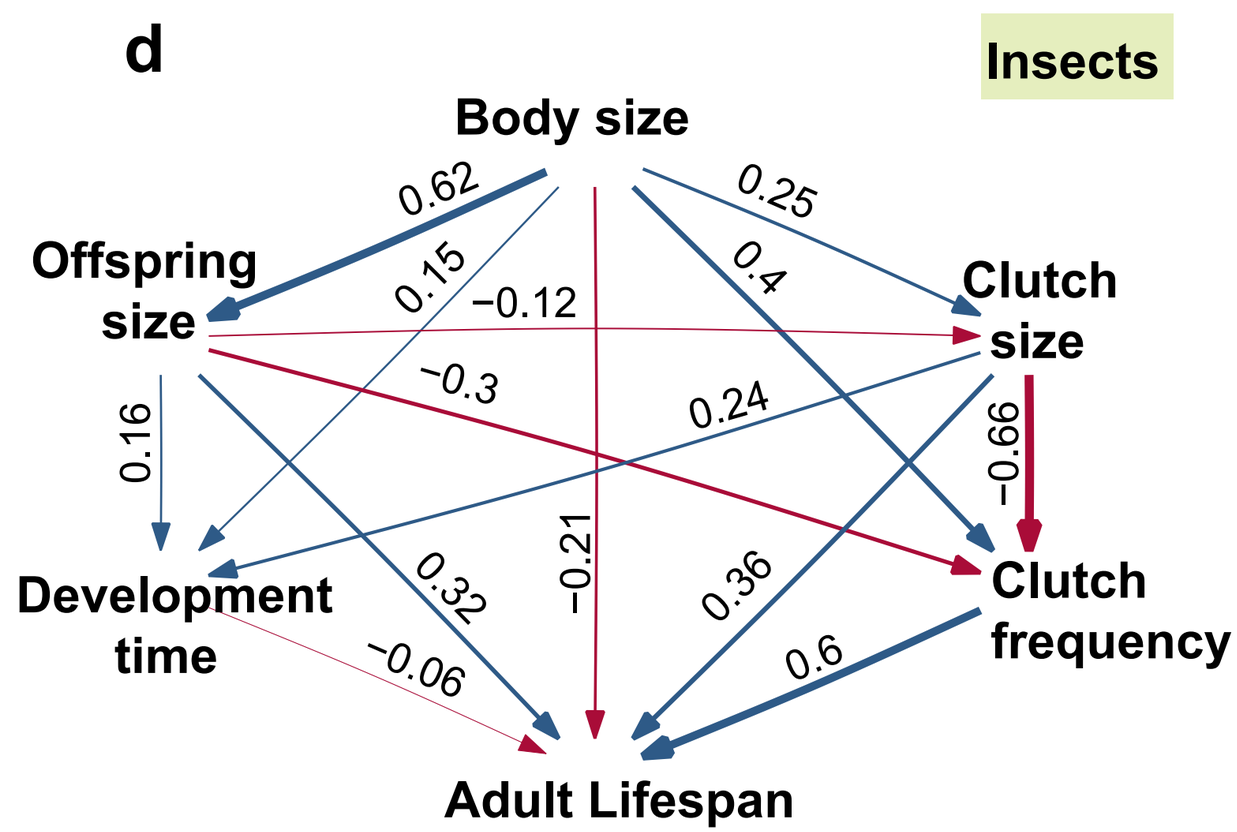
d
Insects
Body size
Offspring size
Clutch size
Development time
Clutch frequency
Adult Lifespan
0.62
0.15
−0.12
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0.4
0.16
−0.3
0.24
−0.66
0.32
−0.21
0.36
−0.06
0.6