A simple offspring-to-mother size ratio predicts post-reproductive lifespan

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Abstract

Why do many animals live well beyond their reproductive period? This seems counter to the theory that the fraction of life spent reproducing should be maximized in order to maximize the number of offspring produced in each generation. To resolve this paradox, hypotheses have been developed that evoke parental or grandparental care as reasons for post-reproductive life (e.g., the Mother and Grandmother Hypotheses). However, these hypotheses fail to explain the presence of post-reproductive life in organisms that do not care for their young, such as *Caenorhabditis elegans*. Here we show that a candidate proxy of the stress of childbirth explains a large portion of the variance in post-reproductive lifespans across many species. A remarkably simple metric, the "offspring ratio" (ratio of the size or weight of offspring to that of the mother) explained 77% of the variance of the post-reproductive lifespan in a sample drawn from widely dispersed taxa. Our results suggest that the stress of childbirth is an important and conserved determinant of post-reproductive lifespan. Thus, long post-reproductive lifespan may simply be a byproduct of the somatic health required for reproduction of large progeny, regardless of parental care.

Keywords: post-reproductive lifespan

Introduction

Although post-reproductive life is often thought of as a result of modern medicine's extensions of lifespan, even before these developments, human females were documented to go through menopause and spend the remainder of their lives without the ability to reproduce ("post-reproductive life") [1,2]. Women who were able to reproduce late in life (without modern reproductive assistance) also lived longer, suggesting a positive correlation between lifespan and reproductive span [3]. Previous work has hypothesized that while connected, reproductive and total lifespan could be under differential control (perhaps even trading off against one another) [4,5], but the reasons for this differential control have not been elucidated [4,5]. In addition to maternal aging effects on progeny quality, the onset of menopause has serious biological implications due to its effects on normal regulatory processes. For example, rates of cancer, cardiovascular disease, and other degenerative processes drastically increase post-menopause [6-8]. Therefore, elucidating the mechanisms that regulate onset of post-reproductive life and subsequent effects on aging has become more critical.

Several theories have been proposed to explain the existence of post-reproductive life through direct or indirect parental care. For instance, the "Mother Hypothesis" theorizes that females stop reproducing in order to concentrate their efforts and resources in raising already-birthed offspring [9,10]. Moreover, the presence of menopause and post-reproductive life can also protect existing offspring by discouraging males from mating with older mothers [11]. The "Grandmother Hypothesis" posits that post-reproductive females assist in the reproductive success of their daughters, through care of grandprogeny [9,12-14]. Mother and Grandmother Hypotheses concentrate upon direct benefits to children and grandchildren.

However, we and others have shown that *C. elegans*, like women, have a proportionally long post-reproductive life span (PRLS), despite the fact that they do not care for their

young [15-19]. In addition, the existence of PRLS has been suggested in studies of brine shrimp (genus *Artermia*), *Drosophila*, *Mabuya buettneri* (the African Skink, a reptile), and other organisms [20-26]. Mother and Grandmother theories cannot account for the long post-reproductive lives of *C. elegans* and other organisms with non-human social structures. The limiting factor of *C. elegans* reproductive span is oocyte quality decline with age, as it is in mammals [16]. Moreover, oocyte quality is governed by similar gene sets in mammals and worms [16], suggesting that factors that regulate reproductive aging may be conserved evolutionarily. Therefore, we wondered whether there is a also conserved determinant of post-reproductive life span (PRLS) across species.

Here we show that such a factor does exist: the ratio of offspring size to mother size correlates well with length of post-reproductive life span across many species. We hypothesize that the offspring ratio may indicate the level of somatic integrity necessary to successfully reproduce, and our tests of this model in *C. elegans* suggest that altering these ratios can have deleterious effects on the mother's survival during reproduction.

Methods

Statistical Analyses: Linear regressions were conducted using native R functionality and the tools available from the "mlbench" package [27,28]. Graphical labels were constructed using the "calibrate" package [29].

Calculations: Several values were computed from the data: Post-Reproductive Lifespan ("PRLS"), Offspring to Maternal Size Ratio ("Offspring Ratio"), Reproductive Window (the proportion of life in which the species can reproduce), Maturity Proportion (the proportion of life spent maturing to reproductive age), Gestational Proportion (the proportion of life spent in gestation in a single reproductive cycle), and Weaning Proportion (the proportion of life spent weaning offspring from one reproductive cycle; only applicable to mammals).

PRLS was computed as the ratio of life after last documented reproduction to maximum documented life expectancy minus maturity time (the final factor facilitates comparisons outside of mammals) [30]. Offspring ratio was computed by taking the ratio of the offspring to maternal size or weight (depending on the data available). When weights were unavailable, the cube of the length of offspring at birth and mother was used. Litter size-adjusted ratio was computed by multiplying the average size of a litter by the offspring ratio. Reproductive Window was computed as the proportion of

maximum lifespan between the age of maturity and reproductive senescence. Maturity Proportion was computed solely for mammals and birds as the ratio of maturation age (for females) to maximum lifespan (the data for non-mammals was not reliable enough). Gestational Proportion was computed similarly as the ratio of gestational time to maximum age.

The equations used to compute the values, then, were as follows:

(1)
$$PRLS = \frac{maximum\ lifespan - age\ at\ last\ birth}{maximum\ lifespan - age\ of\ female\ reproductive\ maturity}$$

(2) †
$$Offspring\ Ratio = \frac{offspring\ weight\ at\ birth}{adult\ weight}\ OR\ \frac{offspring\ length^3}{adult\ length^3}$$

(3) $Litter\ Size\ Adjusted\ Offspring\ Ratio = (Offspring\ Ratio) * (Average\ Litter\ Size)$

(4) ‡
$$Reproductive\ Window = 1 - \frac{Age\ at\ Last\ Birth - Age\ of\ Reproductive\ Maturity}{Maximum\ Age}$$

(5) ‡ $Maturity\ Proportion = \frac{Age\ of\ Reproductive\ Maturity}{Maximum\ Age}$

(6) ‡ $Gestational\ Proportion = \frac{Gestational\ Time}{Maximum\ Age}$

(7) ‡ $Weaning\ Proportion = \frac{Weaning\ Age}{Maximum\ Age}$

†Offspring Ratio was calculated using weights if possible, but if not, lengths were used. If offspring length could not be found, it was approximated using the length of the female gamete (in the case of sea urchins). While among mammals it has been found that length to the fourth power (not third) relates to body weight, the use of logarithmic regression parameters renders the exact exponent irrelevant. Moreover, as a wide range of animals (not just mammals) were studied, it appeared more appropriate to use the natural geometric relationship [31].

‡This is only computed for mammals and some birds. There was not enough non-mammalian information is available to compute a similar value.

Data: A dataset was constructed in order to probe various aspects of animal aging. Data for mammals and most birds (both in captivity and in natural habitats) were primarily obtained from anAge: The Animal Aging and Longevity Database and the references contained therein [32].

Reproductive Senescence data was supplemented using previous reviews of primate and mammalian aging [33-35]. The selection of non-mammalian models was guided by previous aging studies [19,36-39]. Data for the following species were also obtained independently: *Strongylocentrotus franciscanus* (Red Sea Urchin) [40-45], *Strongylocentroltus purpuratus* (Purple Sea Urchin) [41-43,46,47], *Oncorhynchus tshawytscha* (Chinook Salmon) [48-51], *Oncorhynchus kisutch* (Coho Salmon) [49,50,52], *Oncorhynchus keta* (Chum Salmon) [42,49,50,53], *Drosophila Melanogaster* [21-24], *Mabuya buettneri* (African Skink, a reptile) [25,26], *Gallus gallus domesticus* (Leghorn-breed chicken) [54-56], *Galeorhinus galeus* (School Shark) [57-60], and *Alligator mississippiensis* (American Alligator) [61-63]. Different measures of longevity (and their values in various species) were obtained from analyses of the ISIS database of Zoo collections [64].

The following assumptions were made (also made explicit in the data tables): In general, the maximum documented age was either obtained from records or computed by summing the longest possible life history for an animal. Age of maturity and reproductive senescence were found by computing averages of given data. Where given, it was favored to take data from the same paper or source in order to maintain consistency among measurements. However, the sources did not fundamentally disagree with one another—and the results were relatively robust to changes in values. For the three species of salmon and two species of sea urchins, a post-reproductive period of one day was assumed (although the assumption was robust to increasing the PRLS and supported by observations), and age to reproductive maturity was assumed to be negligible in the case of the sea urchins because of their relatively long lives [65]. For the shark and alligator, the age of reproductive senescence was assumed to be the average lifespan of the organism, consistent with previous theoretical and empirical work [66]. In addition, age at reproductive maturity was used from either or both genders when considering all mammals—and separated by gender when considering mammals (due to data limitations). Since not explicit, for sea urchins, litter size and birth size was estimated by the number and size of (female) gametes. Since urchins are external fertilizers, though, we assume that this release is the most stressful part of "birthing" and will suffice.

Data sets:

Datatable 1 (Mammals)
Datatable 2 (All Animals)

Results

To assess whether there is a conserved determinant of post-reproductive life span (PRLS) across species, we gathered information about life history features on a variety of animal taxa (96 species) both within and outside *Mammalia*, including sea urchins, salmon, *Drosophila melanogaster*, and species of reptiles and birds (**Supplemental Table 1; Supplemental Table 2**), for which we could obtain information on reproductive senescence, e.g., life span, age at reproductive maturity, adult size, progeny size at birth, and average litter size (see Supplemental information for all available variables). We then compared these features to the post-reproductive life span ratio (**Figure 1**):

$$PRLS = \frac{maximum\ lifespan - age\ at\ last\ birth}{maximum\ lifespan - age\ of\ female\ reproductive\ maturity}$$

Within mammals, no one factor accounted for the majority of post-reproductive lifespan, perhaps indicating that several different parameters contribute to the determination of post-reproductive lifespan (**Supplemental Table 1**). In addition, humans (data from the hunter-gatherer-like Hadza and !Kung) were not outliers compared to other mammals.

However, a surprisingly simple metric, the ratio of offspring size to mother size, or "Offspring ratio," correlated well with PRLS across the larger set of species. The measure was computed in two ways depending on data available:

$$Offspring\ Ratio = \frac{offspring\ weight\ at\ birth}{adult\ weight}\ OR\ \frac{offspring\ length^3}{adult\ length^3}$$

The unadjusted offspring ratio could explain approximately 75% of the variance of post-reproductive lifespan ($R^2 = 0.771$; $p = 0.000174$) (**Figure 1B**). That is, larger offspring with respect to the mother is associated with longer post-reproductive period of the mother. (Note that while litter size has an inverse and highly correlated ($R^2 = 0.869$) relationship with PRLS (**Figure 1C**), it is also correlated with and inversely related to offspring ratio ($R^2 = 0.781$), and thus cannot be distinguished from offspring ratio (**Figure 1D**).

In order to attempt to separate the effects of phylogeny from taxonomic adaptations, methods outlined previously were utilized [67,68]. Species-level data among mammals were averaged to the family level, recapitulating similar results and suggesting the presence of adaptation. Graphing the residuals of separate offspring and adult weight regressions against PRLS separated the available placental mammal from the single marsupial data point. As for the non-mammals, in

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order to capture more data points, we measured offspring ratio through two methods (outlined in Methods). However, the non-mammals are selected from a wide variety of taxa, and even when some of the closely-related species are averaged (e.g., sea urchins and salmon), the results do not change, lessening the concern about these differences emerging from phylogeny (although methods to separate phylogeny and adaptation are unavailable in this case).

Our comparison of offspring ratio to PRLS also roughly groups organisms by reproductive strategy. Clustered in the low offspring ratio/low PRLS area of the graph are red sea urchins, purple sea urchins, and salmon species—all organisms that release unfertilized gametes into the environment (**Figure 1B**). The African Skink, *Drosophila melanogaster*, School Shark, and Alligator form another group, producing fertilized embryos that are released into the environment with no parental care (**Figure 1B**). Finally, birds and mammals—animals that care for their young—appear to form another cluster at the high offspring ratio/high PRLS region of the graph (**Figure 1B**).
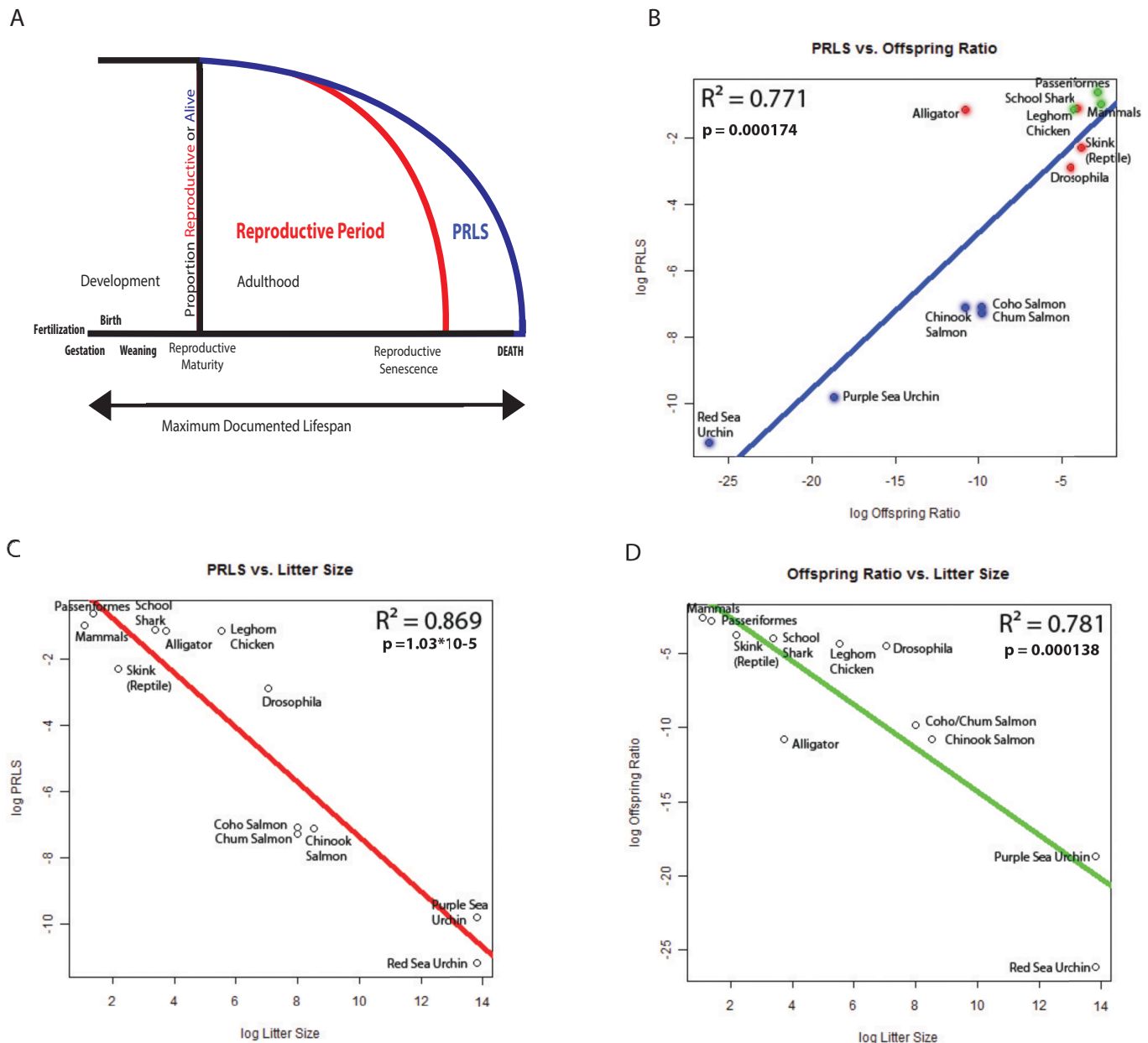
Figure 1. Post-reproductive life span correlates with offspring ratio

When looking at the diversity of animals, it appears that those with the largest offspring ratios have the longest post-reproductive lives, and vice versa. This result is counter to the notion that larger offspring deplete resources, resulting in a shorter post-reproductive life span. Indeed, our results suggest that there is not a direct "tradeoff" between reproductive and post-reproductive life [4]. Instead, we posit that the offspring ratio may be a proxy for stress of childbirth or progeny production. There is likely a point at which an organism cannot devote adequate energy or quality maintenance to reproduction but still has the necessary strength and physical integrity to live. Although in the absence of parental care, neither positive nor negative selection acts on PRLS, these correlations suggest a reason for the particular length of PRLS [5]. In essence, PRLS in many species is simply an unselected residual of life [15,69,70], but the reason for this residual has not been tested previously. We suggest, based on the correlations found here, that more stressful or physically demanding forms of reproduction may require greater strength and integrity in the soma to successfully produce offspring, resulting in greater somatic integrity in the post-reproductive period and correspondingly longer PRLS. The physical manifestation of this threshold can be found when females are pushed to reproduce beyond a typical time: in humans, the most common cause of death of older mothers before the introduction of modern medical interventions was hemorrhaging during childbirth [71]. In the most extreme example in the other direction, sea urchins release millions of one-cell male and female gametes into their environment and reproduce nearly to the end of their ~200 year life span, essentially exhibiting no PRLS.

To test this hypothesis, we perturbed size and reproductive span parameters in *C. elegans*, a model system whose long post-reproductive lifespan has been previously assumed to simply be a lab artifact. [Note: to avoid circularity, we held *C. elegans* out of the correlation analysis in Figure 1.] Our model predicts that if either body size ratio or RS/LS ratio are altered, there would be a suboptimal effect on reproduction or lifespan. TGF-b Sma/Mab mutants are defective in their coupling of longevity and reproductive aging: their germline and oocyte quality is maintained, extending reproductive span (**Figure 2A**), but their somatic tissues age at the same rate as wild-type worms (**Figure 2B**) [15]. Thus, their somatic integrity does not match the high quality of their germlines [16], and their PRLS is compressed without adjusting their offspring ratio proportionally (in fact, their eggs are the same size as wild-type, but their bodies are smaller, thus increasing their offspring ratio) [72]. The effect of this uncoupling is fatal for the animals in late reproduction: because their reproductive span is so long, TGF-b mutants often die from matricide (internal hatching of offspring, **Figure 2C**) while still reproductive, truncating their reproductive lives (**Figure 2D, ***

indicates matricide). Wild-type worms usually avoid this fate: *C. elegans* seems to have tied somatic integrity to the offspring ratio, thus tuning post-reproductive lifespan to maximize reproductive span. Further extension of reproductive span without increased somatic integrity results in matricide.

When would the maintenance of somatic integrity extending through late reproduction be important? Limited nutrient conditions, a common situation in the wild, pose such a situation. Dietary restriction extends the lifespan of all animals tested thus far [73]; additionally, dietary restriction delays reproduction [74] (**Figure 2E**). For example, in mammals, fertilized oocyte implantation can be delayed under low nutrient conditions [75], and in humans this process is modulated through FOXO and Insulin signaling [76,77], which also regulates both lifespan and reproductive span in *C. elegans* (**Figure 2F**). In order for reproduction to resume once nutrients become available, the soma must be healthy enough to enable birth, even at advanced ages. Longevity extension, and thus extended PRLS, under dietary-restricted conditions may simply be the result of the coupling of somatic and reproductive aging that is necessary to allow a plastic reproductive response to varying nutrient conditions.

Discussion

What prevents evolutionary pressure from bringing somatic aging in synchrony with reproductive aging, if for no other reason than to prevent wasting resources that could go to younger generations? For instance, salmon die shortly after spawning; although not instantaneously after reproduction, several days after a multi-year life represents an excellent matching of the two types of aging—despite at least partially separate genetic and regulatory control [69]. Moreover, in the case of salmon specifically, reproduction follows an exhausting migration and severe lack of nutrients (salmon stop feeding), further accelerating somatic decline and death after reproduction [78]. Indeed, lifespan appears to be influenced by hormonal signals (that are in turn partially environmentally influenced) from the reproductive system. For instance, castration of salmon gonads before development prolongs lifespan significantly [79]. Similar findings have been reported in *C. elegans*, mediated through the DAF-12/Nuclear hormone receptor and DAF-16/FOXO signaling pathways [80,81]. Moreover, in humans, the onset of menopause is associated with increased healing time and the rise of cardiovascular disease and other pathologies, and estrogen has been shown to be protective against various health risks—although the mechanisms have not been completely elucidated [82,83].

What remains, though, is to posit why some organisms live very long after they stop reproducing and could theoretically carry another brood. At least a component of this prolonged PRLS could be explained by the nature of biological anti-aging mechanisms. It has been posited that aging is not caused by environmental damage, but rather by the failure to repair that damage [66]. Thus, by that same reasoning, aging depends partly on that damage occurring. If such damage does not occur or occurs more slowly than expected, then aging will be slowed. The case of Werner's syndrome illustrates; the failure of one such repair mechanism takes years to kill—but eventually it does [84].

On the other hand, in addition to repairing damage to the reproductive tract and even the germ line, reproduction requires "positive control." That is, certain processes (hormonal, regulatory, or otherwise) must be allowed for
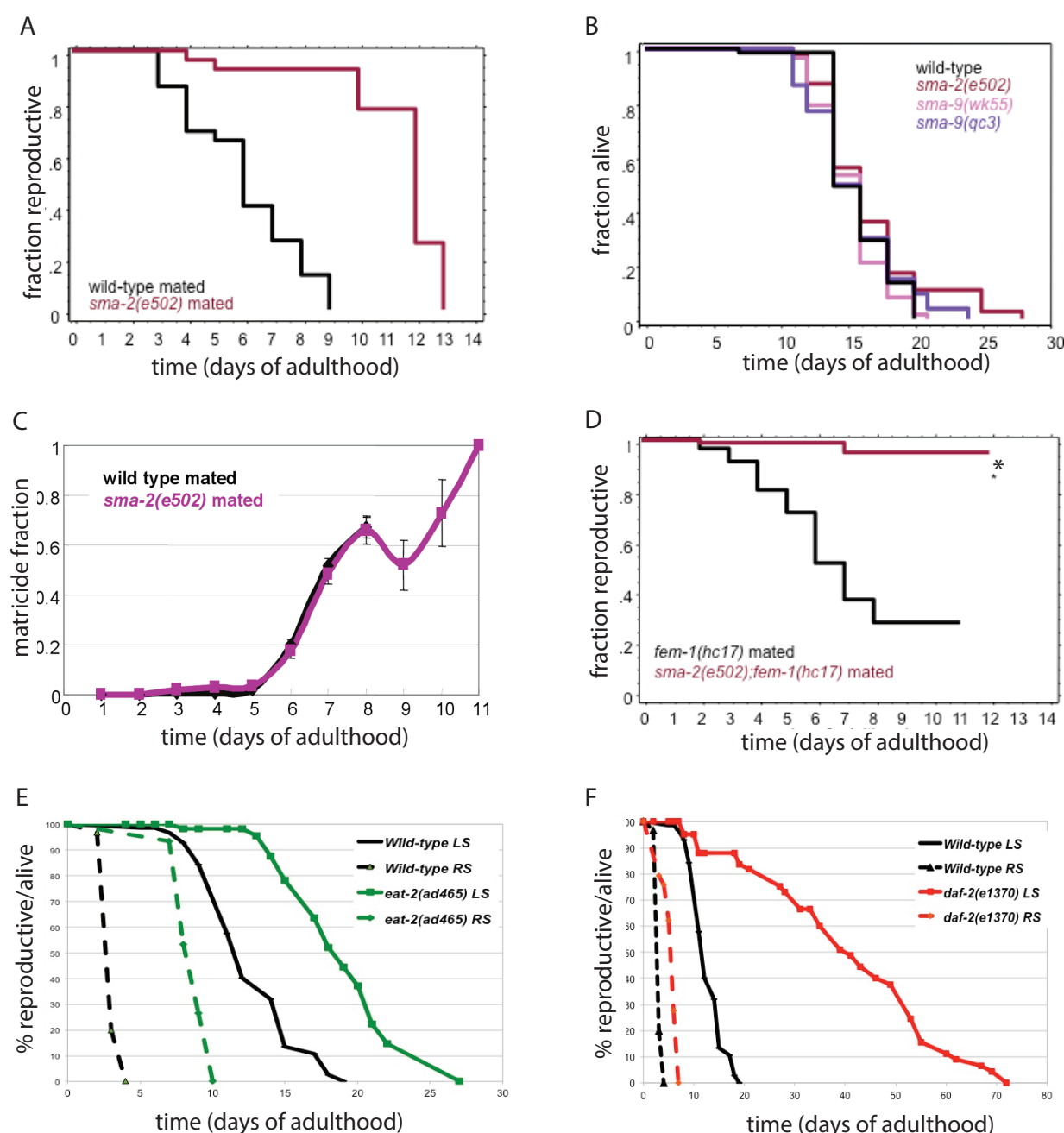

Figure 2. Uncoupling of offspring ratio and reproductive span from longevity results in matricide

reproduction to proceed. If these prerequisites are not met, reproduction halts and the organism enters reproductive senescence. All that has to occur, then, for reproduction to stop—unlike in general somatic aging—is for some prerequisite process to stop or be damaged severely. In a sense, reproduction is much more sensitive to aging because it is a high-stress endeavor and requires so many relatively independent processes at various levels to act. Moreover, these mechanisms are also subject to much greater selection by evolution as they act earlier in life and are intimately concerned with an organism's evolutionary fitness [85]. Nonetheless, this is not to claim that either type of aging is determined. Medical treatments have intervened in both processes. As witnessed by the dramatic increase in lifespan over the 20th century and the development of in vitro fertilization and general reproductive medicine, both mechanisms of aging can be altered. However, oocyte quality ultimately limits human reproductive span, as in *C. elegans* [69]).

The fact that the simple offspring ratio can correlate parameters across a great number of highly unrelated taxonomic groups, from the most primitive to complex animals, suggests deeper relationships at the genetic and regulatory levels, revealing the intricate connection between reproduction and the structure and parameters of life history. Indeed, previous work has suggested that several factors affect PRLS in less developed organisms in which parental care is a less important factor and social structures differ from those of highly developed mammals [86]. Going forward, it will be essential to develop proxies for predation and parental care [87,88], when appropriate, to account for the remaining variance in PRLS. While parental care may certainly modulate the length of post-reproductive life in some animals, considering offspring size ratio as a proxy for childbirth stress, and PRLS as a byproduct of somatic health during reproduction, offers a new perspective in predicting the post-reproductive lifespan across animal taxa. This model explains the existence of post-reproductive lifespan in animals that do not display parental care, disposing of the need to invoke a "purpose" for PRLS in most species.

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Author Contributions

CTM developed the concept; GM carried out all data gathering and analysis; GM and CTM wrote the paper.

Author Information & Financial Interests Declaration

Original data and sources are available in Supplemental Information. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to ctmurphy@princeton.edu.

Abbreviations

PRLS: Post-Reproductive Lifespan, RS: Reproductive Span, LS: Life span

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Figure Legends

Figure 1. Post-reproductive life span correlates with offspring ratio. **A:** Scheme of life history parameters considered distinguishing between reproductive and somatic aging. PRLS = "post-reproductive life span" (from reproductive senescence to death). **B:** Log PRLS is positively correlated with log of the offspring ratio. Regression parameters: Intercept (coefficient estimate: -0.160, standard error: 0.918, t-value: -0.175, and p-value: 0.865) and log offspring ratio: (coefficient estimate: 0.469, standard error: 0.0809, t-value: 5.80, and p-value: 0.000174) on a residual standard error of 1.93, degrees of freedom of 10, R^2 of 0.771, and an F-statistic of 33.58 on 1 and 10 degrees of freedom. **C:** log PRLS is negatively correlated with Litter Size, and **D:** log Offspring Ratio is also negatively correlated with log Litter Size. See **Table 1** for specific regression parameters. All statistical analyses were performed in the R statistical analysis package (64-bit, version 2.14.2). See Supplemental Methods for species information.

Figure 2. **Uncoupling of offspring ratio and reproductive span from longevity results in matricide. A**: The reproductive span of the TGF-b mutant *sma-2* is extended relative to wild-type *C. elegans*, but the life span of TGF-b mutants (*sma-2* and *sma-9*) is not extended (**B**). **C**: Matricide rate of TGF-b mutants (*sma-2*, *sma-9*, and *daf-4*) increases with age. **D**: Matricide (*) causes TGF-b mutant worms to die while still reproductive. (*fem-1* renders the worms spermless, so that all progeny are the result of mating.) **E, F.** The dietary restriction model *eat*-2 and the Insulin/IGF-1-like receptor mutant *daf-2* both have extended reproductive span (RS) and life span (LS). All figures are adapted from Luo, et al. 2009.

Supplemental Information

Supplemental Table 1. A summary of the regressions performed attempting to relate various parameters to PRLS among a sample of mammals. While other variables could explain around 10% of the variance in PRLS, offspring ratio performed the best (IMR was excluded because there were only 7 data points in the regression versus Offspring Ratio's 86.). Nonetheless, litter size and the proportion of life spent in "childhood" (for both males and females) also seem to explain a similar proportion of the variance.

Supplemental Table 2. Summary of the regressions relating various parameters to PRLS among a sample of mammals and a bird, sorted by R^2 value. While other variables could explain around 10% of the variance in PRLS, offspring ratio performed the best. Litter size and the proportion of life spent in "childhood" (for both males and females) explain a similar proportion of the variance. Too few observations of Mortality Rate Doubling time (7) and Increase in Mortality Rate (6) were available to reach significance.

Supplemental Table 3. Summary of data sources.

Supplemental Figure 1. Linear regression of PRLS vs. various variables for 85 mammals distributed across various families and orders. Linear regressions were constructed based on the logarithms of the variable offspring ratio. **A**: PRLS is positively correlated with log of offspring ratio. Regression parameters: Intercept (coefficient estimate: 0.217, standard error: 0.0613, t-value: 3.54, and p-value: <0.000659) and log offspring ratio: (coefficient estimate: -0.0522, standard error: 0.0175, t-value: -2.98, and p-value: 0.00378) on a residual standard error of 0.200, degrees of freedom of 83, R^2 of 0.0956, and an F-statistic of 8.88 on 1 and 83 degrees of freedom. **B, C**: a sampling of regressions of PRLS against other statistically significant variables: average litter size and female maturity proportion. **D-F**: a sampling of regressions of PRLS against other statistically non-significant variables: litter size-adjusted offspring ratio, weaning/adult weights, and metabolic rate, in that order. See **Datatable 1** for specific regression parameters. Mammals from the following families are represented (see supplement for detailed information on species): *Bovidae, Cervidae, Suidae, Tayassuidae, Canidae, Felidae, Herpestidae, Mephitidae, Otariidae, Phocidae, Ursidae, Delphinidae, Phyllostomidae, Rhinolophidae, Vespertilionidae, Dasyuridae, Leporidae, Equidae, Rhinocerotidae, Callitrichidae, Cebidae, Cercopithecidae, Hominidae, Castoridae, Chinchillidae, Dipodidae, Echimyidae, Muridae, Sciuridae*, and *Trichechidae*. All statistical analyses were performed in the R statistical analysis package (64-bit, version 2.14.2).

Supplemental Figure 2. The linear regression of PRLS with litter size-adjusted offspring ratio for the all-animal sample. While the general trend remains (a positive correlation), statistical significance and the ability to explain the variance of the data (R^2) are less than without litter size. Regression of PRLS against offspring ratio and litter size yield similar results. All statistical analyses were performed in the R statistical analysis package (64-bit, version 2.14.2).

Supplemental Figure 3. The Partial Regression Plot of the residuals of PRLS vs. Birth Weight Regression and PRLS vs. Adult Weight Regression for 31 families of placental mammals, 1 family of marsupials, and 1 family of birds. The residuals of the separate regressions (PRLS vs. Birth Weight and PRLS vs. Adult Weight) were plotted against each other to extract any natural groupings with respect to PRLS. While the bird family (Corvidae) was indistinguishable from the placental mammals, the marsupial family (Dasyuridae) marked in red readily separated from the placentals in the top right hand corner. In addition, a group of diverse families (marked in blue), including Manatees (Trichechidae), Chinchillas (Chinchillidae), and New World Monkeys, appear to separate out in the bottom left hand corner. Key: see Data Table 1 (the families represented are stated in Supplemental Figure 1, with the addition of *Corvidae*).

Regressions among All Species							
y-axis[†]	x-axis[†]	R^2	Coefficient Estimate	Coefficient Standard Error	p-value	Residual Standard Error	Degrees of Freedom
PRLS	Litter Size	0.869	-0.823	0.101	1.03×10^{-5}	1.46	10
Offspring Ratio	Litter Size	0.781	-1.46	0.245	0.000138	3.53	10
PRLS	Offspring Ratio	0.771	0.469	0.0809	0.000174	1.93	10
PRLS	Litter-Adjusted Offspring Ratio	0.332	0.565	0.254	0.0500	3.29	10
PRLS	Maturity Proportion	0.0846	0.932	0.969	0.359	3.85	10
[†]Logarithmic transformation of variables unless noted. See supplement for definitions of variables.							
Yellow = t-test of linear regression for selected coefficient is significant at p < 0.05 level							

Table 1. A summary of the regressions relating various parameters to PRLS among a sample of species. Note that litter size and offspring ratio are highly correlated but inversely related.

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Supplemental Table 1: Regressions of Life History and Metabolic Variables (Mammals)						
Variable[†]	R^2	Coefficient Estimate	Coefficient Standard Error	p-value	Residual Standard Error	Degrees of Freedom
IMR[‡] (per year)	0.272	0.0554	0.406	0.230	0.128	5
Offspring Ratio	0.1135	0.0518	0.0158	0.00152	0.179	84
Litter Size	0.0929	0.0945	0.0322	0.00432	0.199	84
Female Maturity Proportion	0.0861	-0.123	0.0438	0.0061	0.200	84
Male Maturity Proportion	0.0844	-0.119	0.0460	0.0114	0.206	73
Growth Rate (per day)	0.0606	0.0364	0.0219	0.103	0.206	43
Litter Size-Adjusted Offspring Ratio	0.0278	-0.0328	0.0211	0.125	0.2059	84
Litters per Year	0.0231	0.0509	0.0392	0.199	0.199	71
Weaning Weight / Adult Weight	0.0217	-0.0405	0.0373	0.283	0.207	53
Gestation Proportion[‡]	0.0207	-0.208	0.156	0.187	0.819	84
Weaning Proportion	0.0184	-0.0394	0.0330	0.237	0.209	76
Birth Weight (g)	0.0166	-0.00820	0.00689	0.238	0.207	84
Body Temperature[‡] (K)	0.0130	0.0942	0.184	0.614	0.960	20
MRDT[‡] (years)	0.00542	-0.00141	0.00780	0.862	0.138	6
Metabolic Rate (W)	0.00291	-0.00512	0.0165	0.758	0.239	33
Weaning Weight (g)	0.00117	0.00256	0.0102	0.804	0.210	53
Adult Weight (g)	0.000140	-0.000740	0.00683	0.914	0.209	84

[†]Logarithmic transformation of variables unless noted. See supplement for definitions of variables.
[‡]For Gestation Proportion, both variables with logarithmically transformed. For IMR and MRDT per year, no logarithmic transformation was performed. For Body Temperature, PRLS was logarithmically transformed.
IMR= Increase in Mortality Rate; MRDT = Mortality Rate Doubling Time
Yellow = t-test of linear regression for selected coefficient is significant at p < 0.05 level
Gray = Too few observations compared to the vast majority of mammalian data; variable is unreliable

Supplemental Table 1. A summary of the regressions performed attempting to relate various parameters to PRLS among a sample of mammals. While other variables could explain around 10% of the variance in PRLS, offspring ratio performed the best (IMR was excluded because there were only 7 data points in the regression versus Offspring Ratio's 86.). Nonetheless, litter size and the proportion of life spent in "childhood" (for both males and females) also seem to explain a similar proportion of the variance.

Supplemental Table 2: Regressions of Life History and Metabolic Variables (Mammals + Bird)						
Variable[†]	R^2	Coefficient Estimate	Coefficient Standard Error	p-value	Residual Standard Error	Degrees of Freedom
Offspring Ratio	0.0972	-0.0526	0.0176	0.00378	0.199	83
Litter Size	0.0909	0.0941	0.0327	0.00504	0.200	83
Female Maturity Proportion	0.0882	-0.125	0.0441	0.00577	0.200	83
Male Maturity Proportion	0.0858	-0.120	0.0463	0.0113	0.207	72
Growth Rate (per day)	0.0573	0.0379	0.0237	0.118	0.208	42
Litter Size-Adjusted Offspring Ratio	0.0304	-0.0345	0.0214	0.110	0.207	83
Litters per Year	0.0231	0.0507	0.0395	0.203	0.200	70
Weaning Weight / Adult Weight	0.0217	-0.0405	0.0373	0.283	0.207	53
Gestation Proportion[‡]	0.0181	-0.199	0.161	0.219	0.824	83
Weaning Proportion	0.0184	-0.0394	0.0330	0.237	0.209	76
Birth Weight (g)	0.0153	-0.00794	0.00699	0.259	0.208	83
Body Temperature[‡] (K)	0.0130	0.0942	0.184	0.614	0.960	20
Metabolic Rate (W)	0.00291	-0.00512	0.0165	0.758	0.239	33
Weaning Weight (g)	0.00117	0.00256	0.0102	0.804	0.210	53
Adult Weight (g)	0.0000258	-0.000321	0.00693	0.963	0.210	83
[†]Logarithmic transformation of variables unless noted. See supplement for definitions of variables.						
[‡]For Gestation Proportion, both variables with logarithmically transformed.						
For Body Temperature, PRLS was logarithmically transformed.						
Yellow = t-test of linear regression for selected coefficient is significant at p < 0.05 level						

Supplemental Table 2. A summary of the regressions relating various parameters to PRLS among a sample of mammals and a bird, sorted by R^2 value. While other variables could explain around 10% of the variance in PRLS, offspring ratio performed the best. Litter size and the proportion of life spent in "childhood" (for both male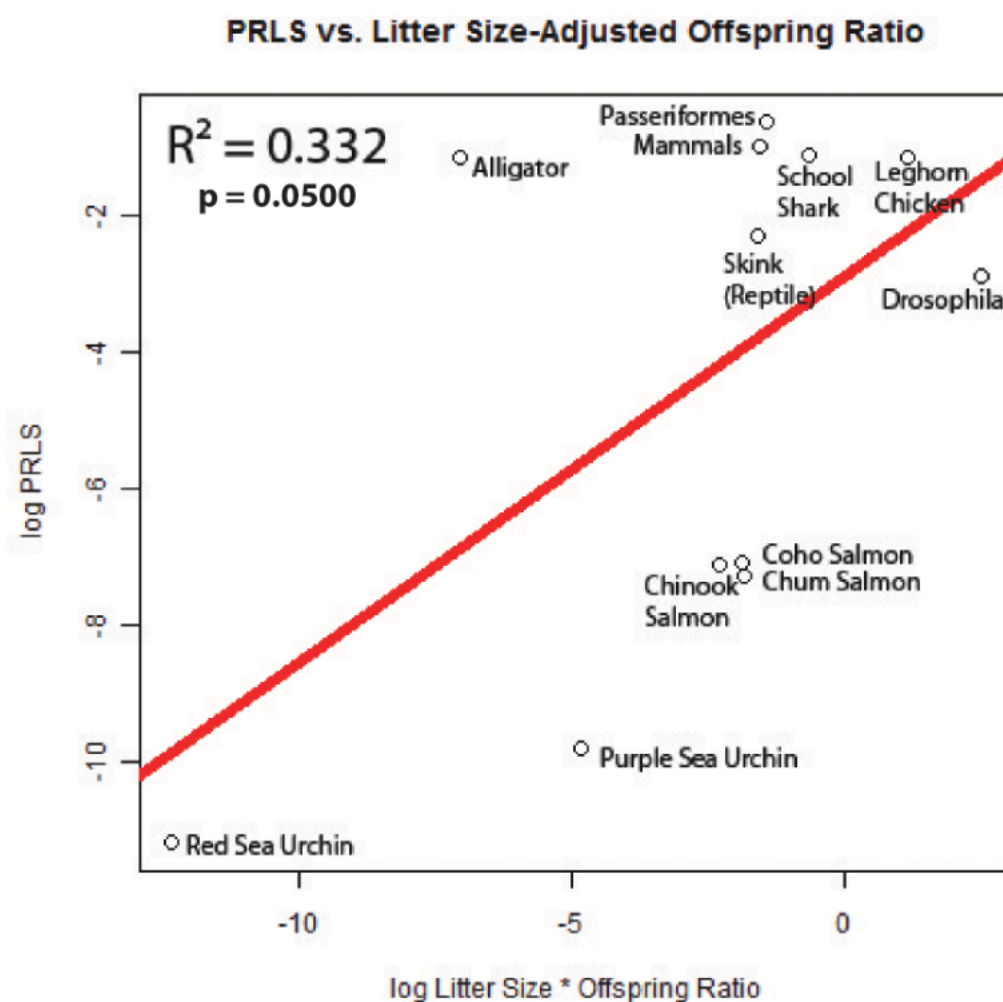s and females) explain a similar proportion of the variance. Too few observations of Mortality Rate Doubling time (7) and Increase in Mortality Rate (6) were available to reach significance.

Supplementary Table 3. Summary of data sources.		
Scientific Name	**Common Name**	**Reference**
Mammals + Some Birds		de Magalhaes and Costa, 2009 Caro et al., 1995 Cohen, 2004 Oli and Dobson, 2003
Strongylocentrotus franciscanus	Red Sea Urchin	Anonymous, 2008 Bodnar, Personal Communication Loram and Bodnar, 2012 Rogers-Bennett, 2007 Sempier, 2003b
Strongylocentroltus purpuratus	Purple Sea Urchin	Anonymous, 2008 Bodnar, Personal Communication Loram and Bodnar, 2012 Rogers-Bennett, 2007 Sempier, 2003a
Oncorhynchus tshawytscha	Chinook Salmon	Allen and Hassler, 1986 Beacham and Murray, 1993 Nicomekl Enhancement Society, 2012 NOAA Fisheries Office of Protected Resources, 2012a
Oncorhynchus keta	Chum Salmon	Beacham and Murray, 1993 Nicomekl Enhancement Society, 2012 NOAA Fisheries Office of Protected Resources, 2012b
Oncorhynchus kisutch	Coho Salmon	Beacham and Murray, 1993 Nicomekl Enhancement Society, 2012 NOAA Fisheries Office of Protected Resources, 2012c
Gallus gallus domesticus	Leghorn-Breed Chicken	California Foundation for Agriculture in the Classroom, 2011 Farm Animal Shelters, 2007 Hermes, 2003
Mabuya buettneri	African Skink	Patnaik, 1994 Smith and Vida, 1990
Drosophila Melanogaster	Fruit Fly/Drosophila	Berrigan, 1991 Schnebel and Grossfield, 1983 Schnebel and Grossfield, 1988 Tatar, 2010
Galeorhinus galeus	School Shark	Baremore, 2010 Food and Agricultural Organization of the United Nations, 1984 Peres and Vooren, 1991 Walker et al., 2006
Alligator mississippiensis	American Alligator	Platt et al., 2004 San Diego Zoo, 2013 Smithsonian National Zoological Park, 2012
Ornithorhynchus anatinus	Duck-Billed Platypus	Cromer, 2004 Hall, 1999 Ojo, 2012

Supplemental Figure 1

PRLS vs. Litter Size-Adjusted Offspring Ratio

Supplemental Figure 2

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Partial Regression Plot: Family Level
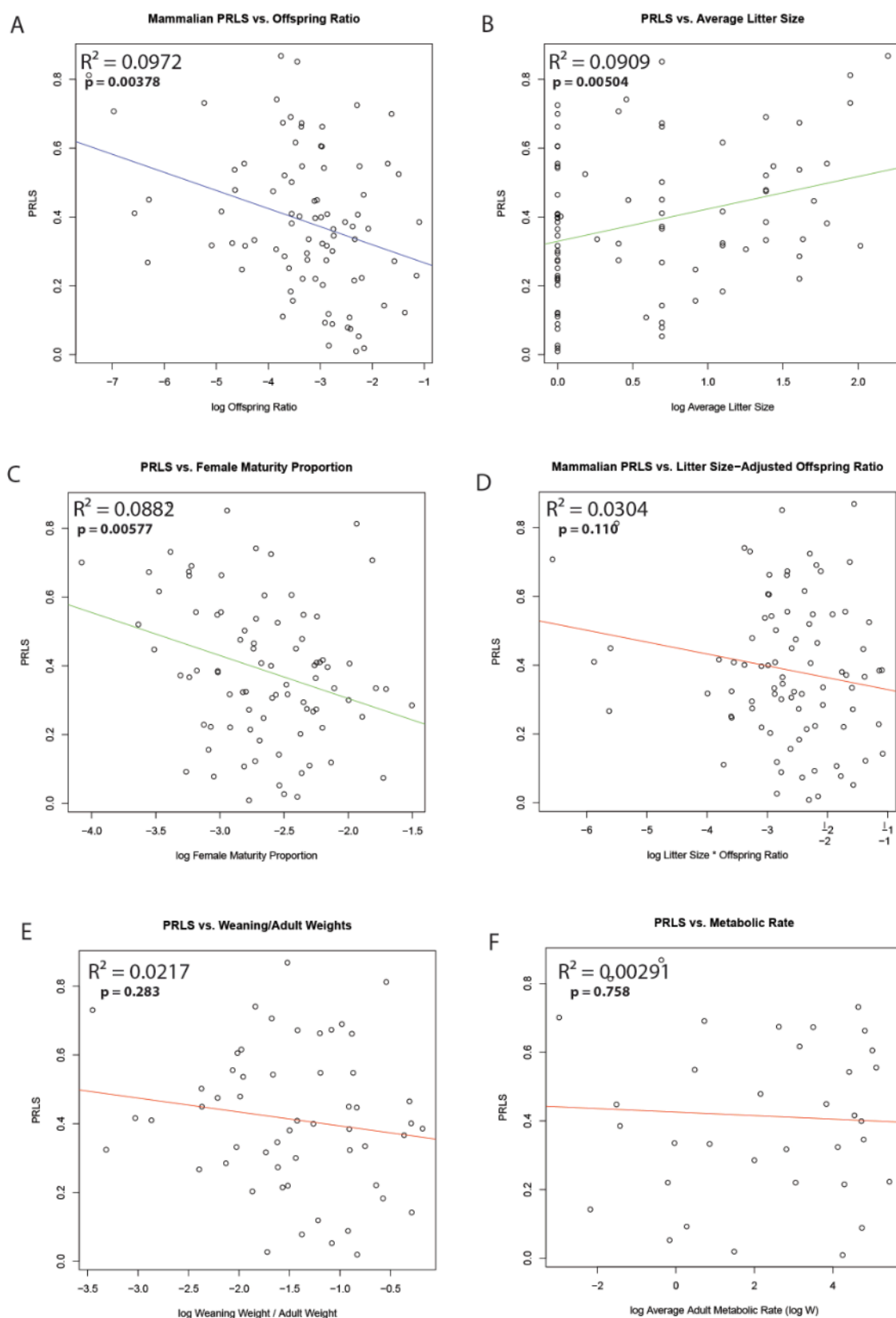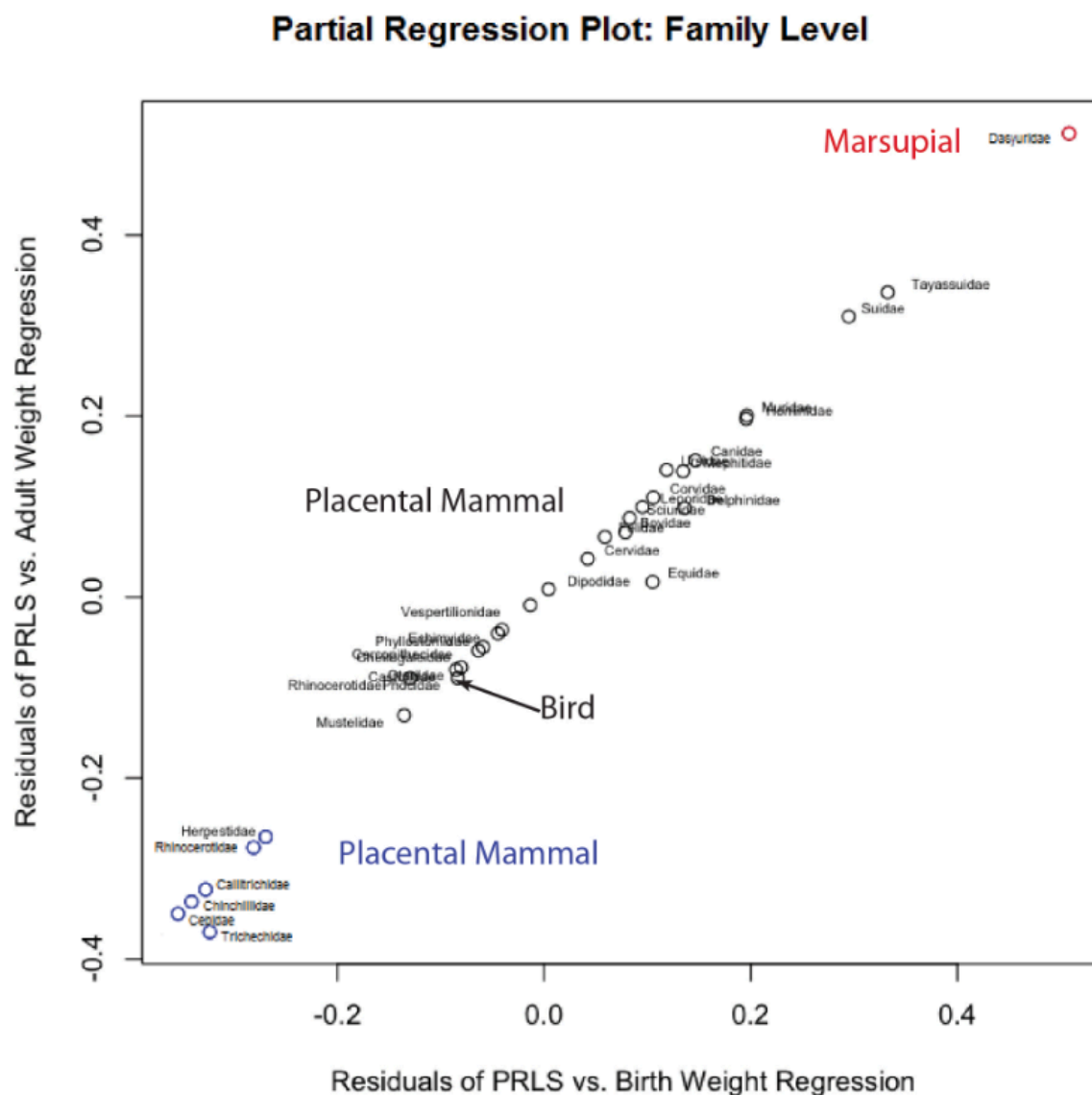
Supplemental Figure 3

Datatable 1

Order	Family	Genus	Species	Common Name	Days to Reach Female Maturity	Female Maturity Proportion	Days to Reach Male Maturity	Male Maturity Proportion
Artiodactyla	Bovidae	Syncerus	caffer	African buffalo	1475	0.135607245	1674	0.153902731
Perissodactyla	Equidae	Equus	asinus	African wild ass	708	0.041270767	1005	0.058583503
Rodentia	Castoridae	Castor	canadensis	American beaver	639	0.074815595	639	0.074815595
Carnivora	Ursidae	Ursus	americanus	American black bear	1278	0.102981467	1278	0.102981467
Carnivora	Phocidae	Pusa	sibirica	Baikal seal	2129	0.104158513	2557	0.125097847
Carnivora	Herpestidae	Mungos	mungo	Banded mongoose	289	0.045504645		
Chiroptera	Vespertilionidae	Eptesicus	fuscus	Big brown bat	547	0.07887527	730	0.105263158
Artiodactyla	Bovidae	Ovis	canadensis	Bighorn sheep	707	0.094028461	749	0.09961431
Rodentia	Sciuridae	Cynomys	ludovicianus	Black-tailed prairie dog	730	0.181818182	730	0.181818182
Artiodactyla	Bovidae	Connochaetes	taurinus	Blue wildebeest	411	0.046338576	912	0.102824285
Carnivora	Felidae	Lynx	rufus	Bobcat	365	0.030959752	730	0.061919505
Primates	Cercopithecidae	Macaca	radiata	Bonnet macaque	1295	0.11826484	1795	0.163926941
Dasyuromorphia	Dasyuridae	Antechinus	stuartii	Brown antechinus	285	0.144596651	285	0.144596651
Carnivora	Ursidae	Ursus	arctos	Brown bear and grizzly bear	1313	0.089931507	1313	0.089931507
Perissodactyla	Equidae	Equus	burchellii	Burchell's zebra	900	0.064888248	900	0.064888248
Sirenia	Trichechidae	Trichechus	manatus	Caribbean manatee	1278	0.062524462	913	0.044667319
Artiodactyla	Cervidae	Rangifer	tarandus	Caribou and reindeer	662	0.083580582	680	0.085853166
Artiodactyla	Bovidae	Rupicapra	rupicapra	Chamois	674	0.104919054	669	0.104140722
Carnivora	Felidae	Acinonyx	jubatus	Cheetah	456	0.060942198	456	0.060942198
Rodentia	Chinchillidae	Chinchilla	lanigera	Chinchilla	240	0.038228735	240	0.038228735
Artiodactyla	Tayassuidae	Pecari	tajacu	Collared peccary	329	0.028614916	358	0.031137204
Chiroptera	Vespertilionidae	Pipistrellus	pipistrellus	Common pipistrelle	456	0.078082192	456	0.078082192
Artiodactyla	Bovidae	Ovis	dalli	Dall's sheep	684	0.095610847	639	0.08932066
Carnivora	Felidae	Felis	catus	Domestic cat	289	0.026392694		
Rodentia	Sciuridae	Tamias	striatus	Eastern chipmunk	187	0.053929344	228	0.065753425
Rodentia	Sciuridae	Sciurus	carolinensis	Eastern gray squirrel	343	0.039818899	401	0.046552124
Chiroptera	Vespertilionidae	Pipistrellus	subflavus	Eastern pipistrelle	212	0.039244724		
Lagomorpha	Leporidae	Lepus	europaeus	European hare	236	0.060427602		
Carnivora	Mustelidae	Mustela	putorius	European polecat	312	0.077008515	322	0.079476737
Carnivora	Mustelidae	Martes	pennanti	Fisher	365	0.06993007	365	0.06993007
Primates	Cercopithecidae	Theropithecus	gelada	Gelada baboon	1391	0.10585997	2190	0.166666667
Carnivora	Ursidae	Ailuropoda	melanoleuca	Giant panda	2192	0.163192376	2192	0.163192376
Rodentia	Muridae	Mesocricetus	auratus	Golden hamster	48	0.033719705	48	0.033719705
Primates	Callitrichidae	Leontopithecus	rosalia	Golden lion tamarin	547	0.047425004	730	0.063291139
Rodentia	Sciuridae	Spermophilus	lateralis	Golden-mantled ground squirrel	637	0.167808219		
Carnivora	Canidae	Urocyon	cinereoargenteus	Gray fox	345	0.058346017	365	0.061728395
Primates	Cheirogaleidae	Microcebus	murinus	Gray mouse lemur	243	0.036579858	243	0.036579858
Carnivora	Phocidae	Halichoerus	grypus	Gray seal	1460	0.093240093	1887	0.120509627
Chiroptera	Rhinolophidae	Rhinolophus	ferrumequinum	Greater horseshoe bat	730	0.06557377	730	0.06557377
Primates	Cercopithecidae	Papio	hamadryas	Hamadryas baboon	1514	0.110611872	1762	0.128730594
Carnivora	Phocidae	Phoca	vitulina	Harbor seal	1095	0.06302521	1460	0.084033613
Artiodactyla	Bovidae	Hemitragus	jemlahicus	Himalayan tahr	547	0.068744502	730	0.091743119
Perissodactyla	Equidae	Equus	caballus	Horse	914	0.043931747	973	0.046767604
Primates	Hominidae	Homo	sapiens	Human	4745	0.106122449	5110	0.114285714
Artiodactyla	Bovidae	Aepyceros	melampus	Impala	456	0.04880137	395	0.042273116
Primates	Cercopithecidae	Macaca	fuscata	Japanese macaque	1483	0.105532823	1369	0.097420388
Cetacea	Delphinidae	Orcinus	orca	Killer whale	3780	0.115068493	4930	0.150076104
Artiodactyla	Bovidae	Kobus	kob	Kob	403	0.050415963	365	0.0456621
Carnivora	Felidae	Panthera	leo	Lion	1095	0.111111111	1095	0.111111111
Chiroptera	Vespertilionidae	Myotis	lucifugus	Little brown bat	210	0.016921837	210	0.016921837
Primates	Cercopithecidae	Macaca	fascicularis	Long-tailed macaque	1238	0.086966739	1544	0.108465051
Rodentia	Dipodidae	Zapus	hudsonius	Meadow jumping mouse	61	0.029843444	61	0.029843444
Artiodactyla	Bovidae	Procapra	gutturosa	Mongolian gazelle	532	0.121461187		
Artiodactyla	Bovidae	Ovis	aries	Mouflon	548	0.065849555	914	0.109829368
Chiroptera	Vespertilionidae	Myotis	myotis	Mouse-eared bat	502	0.062515567	502	0.062515567
Artiodactyla	Cervidae	Odocoileus	hemionus	Mule deer	478	0.059526702	503	0.0626401
Rodentia	Muridae	Onychomys	leucogaster	Northern grasshopper mouse	100	0.048923679	114	0.055772994
Rodentia	Echimyidae	Myocastor	coypus	Nutria	152	0.048992748	152	0.048992748
Carnivora	Mustelidae	Meles	meles	Old World badger	365	0.053763441	365	0.053763441
Lagomorpha	Leporidae	Oryctolagus	cuniculus	Old World rabbit	730	0.222222222		
Cetacea	Delphinidae	Stenella	attenuata	Pantropical spotted dolphin	2983	0.177665277	3956	0.235616438
Primates	Cercopithecidae	Macaca	nemestrina	Pigtail macaque	1125	0.081973186	1095	0.079787234
Passeriformes	Corvidae	Gymnorhinus	cyanocephalus	Pinyon jay	365	0.090909091	365	0.090909091
Carnivora	Ursidae	Ursus	maritimus	Polar bear	1734	0.108463126	1734	0.108463126
Carnivora	Canidae	Nyctereutes	procyonoides	Raccoon dog	304	0.050173296	304	0.050173296
Artiodactyla	Cervidae	Cervus	elaphus	Red deer	852	0.074103066	730	0.063492063
Carnivora	Canidae	Vulpes	vulpes	Red fox	304	0.039102193	304	0.039102193
Rodentia	Sciuridae	Tamiasciurus	hudsonicus	Red squirrel	342	0.095610847		
Primates	Cercopithecidae	Macaca	mulatta	Rhesus monkey	1231	0.084315068	2007	0.137465753
Carnivora	Mustelidae	Martes	zibellina	Sable	456	0.067897558	456	0.067897558
Primates	Callitrichidae	Saguinus	fuscicollis	Saddlebacked tamarin	546	0.06007592	730	0.080321285
Chiroptera	Phyllostomidae	Carollia	perspicillata	Seba's short-tailed bat	258	0.041579371	258	0.041579371
Cetacea	Delphinidae	Globicephala	macrorhynchus	Short-finned pilot whale	3470	0.15090237	5332	0.231876495
Carnivora	Otariidae	Arctocephalus	australis	South American fur seal	1095	0.098039216	2556	0.228847703
Primates	Cebidae	Saimiri	sciureus	South American squirrel monkey	1003	0.090991563	1826	0.165653633
Carnivora	Mephitidae	Mephitis	mephitis	Striped skunk	335	0.066029368	335	0.066029368
Artiodactyla	Bovidae	Damaliscus	lunatus	Topi	639	0.074181565		
Primates	Cercopithecidae	Macaca	sinica	Toque macaque	1460	0.136518771		
Artiodactyla	Bovidae	Kobus	ellipsiprymnus	Waterbuck	771	0.070410959		
Artiodactyla	Cervidae	Capreolus	capreolus	Western roe deer	413	0.064657534	655	0.102544031
Perissodactyla	Rhinocerotidae	Ceratotherium	simum	White rhinoceros	1643	0.100030441	1643	0.100030441
Artiodactyla	Tayassuidae	Tayassu	pecari	White-lipped peccary	548	0.052679644	548	0.052679644
Artiodactyla	Cervidae	Odocoileus	virginianus	White-tailed deer	309	0.039193303	417	0.052891933
Primates	Callitrichidae	Callithrix	jacchus	White-tufted-ear marmoset	477	0.079202989	382	0.063428809
Artiodactyla	Suidae	Sus	scrofa	Wild Boar	334	0.033891426	768	0.077929985
Rodentia	Sciuridae	Marmota	flaviventris	Yellow-bellied marmot	730	0.094339623	730	0.094339623

Number of Days in Gestation	Number of Days to Weaning	Average Litter Size	Number of Litters per Year	Weight at Birth (g)	Weight at Weaning (g)	Weaning Weight/Adult Weight	Adult Weight (g)	Offspring Ratio	Litter-Adjusted Offspring Ratio	Growth Rate (per day)
331	289	1	0.4	44000	166000	0.237142857	700000	0.062857	0.062857	0.0026
359		1		30000			164998	0.18182	0.18182	
128	60	3.5	1	430			20250	0.021235	0.0743225	
70	198	2	0.4	277.5	14050	0.0910859	154250	0.001799	0.003598	0.0029
273	68	1.02	1	3000	66900	0.743333333	90000	0.033333	0.03399966	
60		2.5	2	39			1331.5	0.02929	0.073225	
35		2		3.9	17.2	0.747826087	23	0.169565	0.33913	0.062
180	152	1	1	4400	28000	0.398434721	70275	0.062611	0.062611	0.0031
30	63	4	1	15.75	148.35	0.131866667	1125	0.014	0.056	0.0111
253	278	1	1	18125			164500	0.110182	0.110182	0.0026
65	65	3	0.9	265	1190	0.138372093	8600	0.030814	0.092442	0.0068
161	304	1	1	394	2000	0.29607698	6755	0.058327	0.058327	
30	106	7		0.016	16	0.581818182	27.5	0.000582	0.004074	
103	213	2	0.4	510	26000	0.093693694	277500	0.001838	0.003676	
365	395	1	0.6	32000	205000	0.732142857	280000	0.114286	0.114286	0.0038
335	456	1	0.4	32000			322000	0.099379	0.099379	0.0024
228	120	1	1	6500	20000	0.197530864	101250	0.064198	0.064198	0.0047
122	76	1	1	2400			37500	0.064	0.064	
88	107	3	0.7	489	1940	0.036261682	53500	0.00914	0.02742	
111	54	2	2	35			642.5	0.054475	0.10895	
145	49	2	2	700	4881	0.241633663	20200	0.034653	0.069306	
42	42	1.2		1.125			5	0.225	0.27	0.0668
173	129	1	1	2819			73100	0.038564	0.038564	
65	56	4		97.5			3900	0.025	0.1	
31	36	5	1.5	3.4	50.5	0.526041667	96	0.035417	0.177085	
44	66	4	2	15	200	0.375234522	533	0.028143	0.112572	0.0234
44		2		0.94	5.2	0.693333333	7.5	0.125333	0.250666	
42	29	2	3.8	119.67	390	0.093413174	4175	0.028663	0.057326	0.0191
42	63	7.5	1.5	9.5			809	0.011743	0.0880725	0.0328
45	66	2.5	1	35			3175	0.011024	0.02756	
168	433	1	0.5	464	3900	0.240740741	16200	0.028642	0.028642	
48	182	1.5	0.7	110	22000	0.187234043	117500	0.000936	0.001404	0.0028
16	20	9	3	2.45	22.93	0.218380952	105	0.023333	0.209997	0.0574
128	131	2	1.8	55.3	165	0.25210084	654.5	0.084492	0.168984	0.0077
30	37	5.12	0.94	6.26	74.2	0.470812183	157.6	0.039721	0.20337152	0.0411
57	55	4	1	95	519.7	0.109410526	4750	0.02	0.08	0.0127
61	37	2	1	6			64.8	0.092593	0.185186	0.0362
240	19	1	0.9	14000	41450	0.154664179	268000	0.052239	0.052239	
80	60	1		5.8			22.875	0.253552	0.253552	
171	300	1	0.8	814	3950	0.219444444	18000	0.045222	0.045222	0.0026
253	30	1	1	11000	23945	0.208217391	115000	0.095652	0.095652	0.0013
183	151	1	1	2000			35200	0.056818	0.056818	
337	274	1		79200			250000	0.3168	0.3168	
280	639	1	0.3	3312.5	11750	0.189409204	62035	0.053397	0.053397	0.0005
198	167	1	1	5550	15900	0.302857143	52500	0.105714	0.105714	0.0043
174	366	1.5	0.5	496	1767	0.198930481	8882.5	0.05584	0.08376	
435	471	1	0.2	180000			3990000	0.045113	0.045113	
251	189	1	1.3	5405	31600	0.300952381	105000	0.051476	0.051476	
109	216	3	1	1300	8480	0.048457143	175000	0.007429	0.022287	0.0035
55	25	1		1.96			10	0.196	0.196	0.116
165	242	1	0.9	320	848.4	0.133343811	6362.5	0.050295	0.050295	
19	28	5.5	2.1	0.8	7.8	0.433333333	18	0.044444	0.244442	0.0328
185		1.3	1	2900			30000	0.096667	0.1256671	
146	182	1.58	1	2370	17500	0.159090909	110000	0.021545	0.0340411	
65	42	1		5.9			28.55	0.206655	0.206655	0.109
207	132	1.5	1	2950	23100	0.405263158	57000	0.051754	0.077631	0.0057
31	23	4	2.5	2.6	13.1	0.403076923	32.5	0.08	0.32	0.0634
131	91	6	2.3	225	1750	0.222929936	7850	0.028662	0.171972	
49	90	3	1	80			13000	0.006154	0.018462	0.0196
30	26	5	4.3	45	214	0.118888889	1800	0.025	0.125	0.0228
345	543	1	0.3	10000			112500	0.088889	0.088889	
172	324	1	0.8	462.5	1416.5	0.179020537	7912.5	0.058452	0.058452	0.0015
17		4	1	6.26			105	0.059619	0.238476	0.303
230	303	2	0.4	665	27000	0.056842105	475000	0.0014	0.0028	0.0022
61	47	6	1	75	825	0.126923077	6500	0.011538	0.069228	
245	156	1	0.9	10100	56500	0.2825	200000	0.0505	0.0505	0.006
52	48	5	1	100	1397	0.338117482	4131.7	0.024203	0.121015	0.0177
37	63	4.2	1.7	7	83.8	0.419	200	0.035	0.147	0.0216
165	292	1	1	464	1454	0.176563449	8235	0.056345	0.056345	0.0012
30	56	3		30	600	0.562482422	1066.7	0.028124	0.084372	
147	91	1.8	1	39.9			456.5	0.087404	0.1573272	
95		1		5	12.5	0.833333333	15	0.333333	0.333333	0.0347
452	730	1	0.2	60000			2200000	0.027273	0.027273	
236	411	1	1	4250			110000	0.038636	0.038636	
161	177	1	1	107	403	0.435675676	925	0.115676	0.115676	0.0125
63	60	5	1	33.5	493.5	0.141	3500	0.009571	0.047855	0.0143
238		1	0.6	11100			110000	0.100909	0.100909	
152	396	1	0.7	446			4370	0.102059	0.102059	
264	213	1	1	9000			175333	0.051331	0.051331	
153	89	1.6	1	1010	8692.5	0.40119169	21666.7	0.046615	0.074584	
515	365	1	0.4	52500			2180000	0.024083	0.024083	
158	50	2		700			22000	0.031818	0.063636	
198	129	2	1	3000	36000	0.413793103	87000	0.034483	0.068966	0.007
144	62	2	2	26.5	86.67	0.339615987	255.2	0.10384	0.20768	0.0172
115	56	7	1.5	960	5700	0.031666667	180000	0.005333	0.037331	0.0095
30	33	4	0.9	33.8	479	0.136857143	3500	0.009657	0.038628	

Maximum Age (years)	Maximum Age (days)	Age of Reproductive Senescence (Days)	PRLS	Increase in Mortality Rate (per year)	Mortality Rate Doubling Time (Years)	Basal Metabolic Rate (W)	Body Temperature (K)
29.8	10877	6570	0.301212508				
47	17155	7300	0.556150058			164.92	
23.4	8541	5475	0.307137434				
34	12410	8151.545	0.267737603				
56	20440	10950	0.401998799				
17.4	6351	5110	0.15704388				
19	6935	5475	0.142924233			0.113	309.15
20.6	7519	6205	0.089107457			114.674	311.15
11	4015	2190	0.333333333			2.358	
24.3	8869.5	6570	0.223266537			230.073	311.15
32.3	11789.5	4380	0.616613419			23.446	
30	10950	8503	0.119316416				
5.4	1971	315	0.81316726			0.189	308.25
40	14600	7300	0.450590803				
38	13870	6935	0.465304549				
56	20440	18980	0.009497965			70.0056	
21.7	7920.5	4745	0.346283667			119.66	
17.6	6424	3650	0.365217391				
20.5	7482.5	4745	0.324699352			61.77	312.15
17.2	6278	5475	0.093242796			1.31	
31.5	11497.5	3650	0.673187984			33.165	310.65
16	5840	2555	0.525445765	0.36	4		
19.6	7154	4562.5	0.294822257	0.05	1.5		
30	10950	5110	0.520682863				
9.5	3467.5	2555	0.221155312			0.813	311.35
23.6	8614	2555	0.691089348			2.062	311.85
14.8	5402	3285	0.367052023				
10.7	3905.5	1825	0.502657038				
11.1	4051.5	2555	0.316753577				
14.3	5219.5	3650	0.248120301				
36	13140	6935	0.409736999				
36.8	13432	3285	0.707740214				
3.9	1423.5	180	0.869138495			0.69	311.25
31.6	11534	10122	0.078729407				
10.4	3796	2098.75	0.335628363			0.967	309.45
16.2	5913	2920	0.475574713				
18.2	6643	4015	0.37265625				
42.9	15658.5	11315	0.203084833				
30.5	11132.5	9125	0.122807018				
37.5	13687.5	9490	0.220437836	0.06	4	21.095	
47.6	17374	12775	0.215246637			73.29	
21.8	7957	4380	0.408906883				
57	20805	15330	0.229299683	0.0002	4		
122.5	44712.5	18250	0.543378995	0.0002	8	82.78	310.15
25.6	9344	4015	0.548267327				
38.5	14052.5	9125	0.274036358				
90	32850	17520	0.397316821		14		
21.9	7993.5	2555	0.663395033				
27	9855	5110	0.416666667			94.58	311.05
34	12410	3650	0.700819672			0.051	
39	14235	5110	0.606832346				
5.6	2044	1095	0.447806354			0.219	
12	4380	2555	0.336018711				
22.8	8322	2007.5	0.74176743				
22	8030	5475	0.272715197				
22	8030	5110	0.323358051				
5.6	2044	1195	0.385288066				
8.5	3102.5	1825	0.381460769				
18.6	6789	4380	0.318181818			16.647	310.15
9	3285	1825	0.285714286			7.395	312.15
46	16790	12775	0.074744695				
37.6	13724	12255.4	0.027272006				
11	4015	1898	0.48				
43.8	15987	8395	0.411001193				
16.6	6059	2555	0.556038228				
31.5	11497.5	6387.5	0.399981213			112.43	
21.3	7774.5	2433.33333	0.674274369			13.731	311.85
9.8	3577	1460	0.548686244			1.615	311.85
40	14600	9125	0.317450819	0.02	15		
18.4	6716	5110	0.18370607				
24.9	9088.5	7619.5	0.108047995				
17	6205	3650	0.386245166			0.24	309.55
63	22995	14600	0.252240717	0.017	20		
30.6	11169	7300	0.275362319				
30.2	11023	9824.4	0.019520958			4.429	311.15
13.9	5073.5	2190	0.537828427				
23.6	8614	2190	0.72539185				
29.3	10694.5	5475	0.407114625				
30	10950	4015	0.605560468			148.949	
17.5	6387.5	3285	0.450163194			46.347	311.15
45	16425	13140	0.111081045				
28.5	10402.5	1460	0.851844335				
21.6	7884	2555	0.662706271			123.447	312.15
16.5	6022.5	5251	0.053106122			0.848	309.15
27	9855	2555	0.731645836			104.15	
21.2	7738	3650	0.479166667			8.626	309.65

Datatable 2

Name	Age of Reproductive Senescence	Age of Maturity	Maturity Proportion (yrs)	Max Age	PRLS	Birth Weight or Size	Adult Weight or Size	Offspring Ratio	Litter Size	Litter-Adjusted Offspring Ratio
Strongylocentrotus franciscanus	max - 1day*	1.5yrs	0.0075	200yrs	1.38E-05	0.01cm	61cm	4.41E-12	1000000	4.41E-06
Strongylocentroltus purpuratus	max - 1day*	2yrs	0.04	50yrs	5.71E-05	0.01cm	5cm	8.00E-09	1000000	8.00E-03
Oncorhynchus tshawytscha	max - 1day*	4.65yrs	0.58125	8yrs	8.18E-04	361g	18kg	2.01E-05	5021	1.01E-01
Oncorhynchus keta	max - 1day*	3yrs	0.428571	7yrs	0.000694	276g	5.2kg	5.32E-05	2967	1.58E-01
Oncorhynchus kisutch	max - 1day*	2.75yrs	0.458333	6yrs	8.43E-04	193g	3.6kg	5.35E-05	2915	1.56E-01
Gallus gallus domesticus	2.5yrs	19wks	0.091346	4yrs	0.312169	53.3g	4077g	0.013073	250	3.27E+00
Passeriformes	5.2yrs	1yr	0.090909	11yrs	0.527	6.26g	105g	0.059619	4	2.38E-01
Mabuya buettneri	1month	2month	0.166667	1yr	0.1	0.367g	16.2g	0.022637	9	2.04E-01
Drosophila Melanogaster	50.5days	7.5days	0.141509	53days	0.054945	9.7microgram	0.9mg	0.010778	1137	1.23E+01
Mammals	15.8yrs	2.30yrs	0.083333	27.6yrs	0.375494	7634g	161865g	0.071765	3	2.15E-01
Galeorhinus galeus	41yrs	12.5yrs	0.227273	55yrs	0.329412	35cm	134cm	0.017819	29	0.516759
Alligator mississippiensis	45yrs	12yrs	0.2	60yrs	0.3125	71.2mm	2600mm	2.05E-05	42.5	0.000873