Diet mediates the relationship between longevity and reproduction in mammals

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Abstract The disposable soma hypothesis posits a negative correlation between longevity and reproduction, presumably because these aspects of fitness compete for a limited pool of nutrients. However, diet, which varies widely among animals, could affect the availability of key nutrients required for both reproduction and longevity, especially protein. We used a comparative database of mammal life history data to test the hypothesis that carnivores experience less of a negative relationship between reproduction and longevity than herbivores. Annual reproduction and adult mass were significant predictors of longevity among all mammals; although, the relative importance of reproduction and mass for explaining longevity varied among trophic levels. In herbivores, reproduction was a stronger predictor of longevity than mass. Carnivores showed the

opposite pattern with reproduction explaining much less of the variation in longevity. Omnivores showed an intermediate pattern with mass and reproduction explaining similar amounts of variation in longevity. In addition, longevity and reproduction were significantly higher in omnivores than herbivores and carnivores, which were not different from each other. Higher dietary protein at higher trophic levels may allow mammals to avoid potential conflicts between reproduction and longevity. However, there may be potential costs of carnivorous diets that limit the overall performance of carnivores and explain the peak in reproduction and longevity for omnivores.

Keywords Mammal · Disposable soma theory · Trophic level · Diet

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Animals differ widely in aging and longevity. While size is known to be a major predictor of longevity, even similarly sized animals can vary widely in their lifespan (Speakman 2005a). For example, mice live up to 5 years, while similarly sized bats can live over 30 years (Wilkinson and South 2002; De Magalhães and Costa 2009). Comparative analyses can identify the ecological and evolutionary factors related to variation in longevity among closely related animals and guide research on model systems or paired comparisons to elucidate the physiological mechanisms that

underlie these differences in longevity (Austad 1997; Ricklefs 2008; Austad 2009, 2010).

There are several explanations for why species differ in lifespan (Ricklefs 1998; Kirkwood and Austad 2000; Speakman 2005a; Monaghan et al. 2008). In some species, high levels of extrinsic mortality due to disease, predation, or abiotic pressures may result in low levels of selection for longevity-enhancing traits, which would not have a chance to be expressed in nature (Williams 1957; Williams et al. 2006; Ricklefs 2010). This extrinsic mortality hypothesis has been used to explain the significantly higher lifespans of flying or arboreal animals, especially birds and bats, which may have lower mortality due to predation compared to similarly sized non-flying animals (Austad and Fischer 1991; Wilkinson and South 2002; Shattuck and Williams 2010; Wasser and Sherman 2010).

The disposable soma theory is another hypothesis that can explain variation in longevity among species (Kirkwood 1977; Kirkwood and Holliday 1979; Kirkwood 1997, 2002). This theory proposes that somatic maintenance, which affects lifespan, and reproduction are activities that compete for a limited pool of energy and nutrients (Cichon 1997; Kirkwood 2002). As a consequence, variation in longevity can arise from differences in the relative allocation of energy and nutrients to somatic maintenance versus reproduction, either on a small scale (e.g., investment in a current clutch) or larger scale (e.g., semelparity vs. iteroparity). A negative correlation between reproduction and longevity has been reported in many animals (Williams 1966; Reznick 1985, 1992; Harshman and Zera 2007).

We postulated that one mechanism for the tradeoff of resources between longevity and reproduction put forward by the disposable soma theory (Kirkwood 1977; Kirkwood and Holliday 1979; Kirkwood 1997, 2002) is the availability of key nutrients, such as dietary protein. A high availability of key nutritional resources could allow animals to invest heavily in reproduction with less of a sacrifice to longevity or vice versa. Protein, in particular, is an important building block both for maintenance and reproduction, can also be catabolised for energy and can vary widely in the diet of animals depending upon their trophic level (i.e., herbivores, omnivores, and carnivores).

We used a large comparative database to test if trophic level influenced the relationship between longevity and reproduction of mammals. These analyses

included mass as a factor since mass is a strong predictor of both longevity and reproduction (e.g., Speakman 2005a; Ricklefs 2010). The disposable soma hypothesis predicts that there should be a strong negative relationship between longevity and reproduction (i.e., investment of energy and nutrients in reproduction comes at a cost of longevity). However, if higher protein in an animal's diet eases the tradeoff between reproduction and longevity, then, we would predict less of a negative relationship between longevity and reproduction in carnivores compared to herbivores.

Methods

We collected data on maximum longevity, adult body mass, litter size, and number of litters per year of a wide range of mammal species from “AnAge: The Animal Aging & Longevity Database” (<http://genomics.senescence.info/species/>; De Magalhães and Costa 2009). Our analyses included all species of mammals for which data were available on all four measurements and consisted of data for 247 species of herbivores, 117 omnivores, and 118 carnivores from 86 families and 20 orders.

Sample size of individuals used for each species record is an important consideration in studies of maximum longevity (Krementz et al. 1989). Species records in the AnAge database should be sufficient to estimate maximum longevity since the majority of the species records (i.e., 59%, 284 species) were based on data from over 100 individuals, and most others (i.e., 34%, 166 species) were based on data from 10 to 100 individuals. Maximum longevity has also been criticized because the values can be quite large compared to average lifespan. Nevertheless, while the relevance of the value of maximum longevity for the lifespan of an average individual is debatable, it does provide a metric that can be compared to examine relative differences in lifespan among trophic levels.

We supplemented this database on maximum longevity and aging with information on the diet of mammal species (Nowak 1999). Mammals were categorized as herbivores if at least two thirds of their diet consisted of plant material such as leaves, seeds, and fruit (i.e., animal material was only rarely or never included in their diet), carnivores if at least two thirds of their diet consisted of animal material, and omnivores for all intermediate species (i.e., if both plant and animal material were significant contributions to their diet). For

example, among the bears (Carnivora, Ursidae), pandas (*Ailuropoda melanoleuca*) were classified as herbivores, grizzly and black bears (*Ursus arctos* and *Ursus americanus*) as omnivores, and polar bears (*Ursus maritimus*) as carnivores.

Data were analyzed both using species as data points and using phylogenetically controlled analyses (Grafen 1989; Speakman 2005b; Ricklefs 2008). Our measure of reproduction was calculated as annual offspring production, which was simply the product of litter size and the number of litters per year. Body mass was included in the analyses and log-transformed due to its allometric scaling with longevity and aging (e.g., Speakman 2005a, b; Lindstedt and Calder 1981). Maximum longevity was also log-transformed. We conducted a 3-factor general linear model analysis of variance (ANOVA) to test the separate and interactive effects of diet, mass, and reproduction on longevity. We used surface plots to visualize the relationships between the three predictor variables (diet, mass, and reproduction) and longevity. The surface plots were thin-plate splines fitted to the data using the FIELDS package in R (version 2.5.1). Separate plots were calculated for each trophic level with mass on the x-axis, reproduction on the y-axis, and longevity as changes in color with isolines to aid in visualizing changes in longevity.

Phylogenetically controlled analyses were conducted using the “phylogenetic regression” method of Grafen (1989), which is the phylogenetic equivalent of a general linear model ANOVA. The mammalian phylogenetic information included in the AnAge database was used in the phylogenetic regression and branch lengths were calculated using both the default and proportionally scaled methods, although the branch lengths used had very little effect on *p* values. In phylogenetic regression, model effects have to be specified individually with both an effect and control and the specific model used to test two-way interactions can vary depending upon the terms chosen for the control. While different styles of model building can be used to justify particular combinations of control terms, for transparency, we provided the results of two-way interactions with all possible control terms.

Results

Overall, there was a significant effect of trophic level on longevity. Omnivores had significantly higher

longevity than both herbivores and carnivores, which were not significantly different from each other (Fig. 1a). Mass and reproduction were also significant predictors of longevity on their own in both ANOVA and phylogenetically controlled ANOVA tests (Table 1). As predicted, there was a significant positive relationship between mass and longevity and a significant negative relationship between reproduction and longevity. There were also significant two- and three-way interactions between diet, mass and reproduction on longevity (Table 1). The two-way interactions between diet and reproduction and between mass and reproduction both received some support from phylogenetically controlled analyses (Table 2). The three-way interaction did not receive support in phylogenetically controlled analyses (Table 2), although there may be limited power to detect

Fig. 1 Least-squared means of **a** log longevity (taking into account log mass and reproduction) and **b** reproduction (taking into account log mass and log longevity) for mammals with herbivorous, omnivorous, and carnivorous diets. Bars with different letters were statistically different from each other in post-hoc tests

Table 1 Statistical results testing the effects of diet, reproduction, and mass on longevity of mammals using analysis of variance

Effect	<i>df</i>	<i>F</i>	<i>P</i>
Diet	2,470	4.49	0.01
Reproduction	1,470	10.11	0.002
Mass	1,470	298.57	<0.0001
Diet×reproduction	2,470	5.55	0.004
Diet×mass	2,470	9.04	0.0001
Reproduction×mass	1,470	4.68	0.03
Diet×reproduction×mass	2,470	8.76	0.0002

a three-way interaction in this phylogenetically controlled analysis.

We examined the nature of the interactions between variables using partial correlation coefficients (PCC), which quantified the relative contribution of reproduction and mass in explaining longevity separately for herbivores, omnivores, and carnivores. In herbivores, reproduction (PCC=0.50) was the major predictor of longevity and mass (PCC=0.06) was relatively less of a predictor while, in carnivores, mass (PCC=0.50) was a much stronger predictor of longevity than reproduction (PCC=0.14). Omnivores showed an intermediate pattern

with a relatively similar contribution of reproduction (PCC=0.55) and mass (PCC=0.40) in explaining longevity. Changes in the relative explanatory power of reproduction and mass for longevity were also apparent in three-dimensional plots (Fig. 2). In herbivores, changes in longevity occurred strongly on the reproduction axis and also on the mass axis (i.e., color, which represents longevity, grades vertically and also horizontally; Fig. 2). However, in carnivores, there was much less of a change in longevity associated with the reproduction axis, and most of the change in longevity was associated with changes in mass (i.e., color mostly

Table 2 Statistical results testing the effects of diet, reproduction, and mass on longevity of mammals using phylogenetically controlled analysis of variance

		Branch lengths	Default		Scaled	
Effect	Control	<i>df</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Diet	Mass repro	2,141	5.22	0.006	4.94	0.008
Reproduction	Mass diet	1,140	12.05	<0.001	10.97	0.001
Mass	Repro diet	1,140	136.86	<0.001	103.97	<0.001
Diet×mass	Diet, repro, mass	2,140	2.11	0.13	2.78	0.07
	Diet, repro, mass, diet×repro	2,138	1.18	0.31	1.70	0.19
	Diet, repro, mass, mass×repro	2,139	1.32	0.27	1.87	0.16
	Diet, repro, mass, diet×repro, mass×repro	2,137	1.18	0.31	1.94	0.15
Diet×reproduction	Diet, repro, mass	2,140	4.21	0.02	4.03	0.02
	Diet, repro, mass, diet×mass	2,138	2.30	0.10	2.70	0.07
	Diet, repro, mass, mass×repro	2,139	0.81	0.45	1.32	0.27
	Diet, repro, mass, mass×repro, diet×mass	2,137	0.57	0.56	1.27	0.28
Mass×reproduction	Diet, repro, mass	1,141	17.41	<0.001	17.47	<0.001
	Diet, repro, mass, diet×mass	1,139	15.73	<0.001	15.12	<0.001
	Diet, repro, mass, diet×repro	1,139	12.37	<0.001	12.33	<0.001
	Diet, repro, mass, diet×repro, diet×mass	1,137	13.16	<0.001	13.13	<0.001
Diet×mass×reproduction	Diet, repro, mass, diet×repro, diet×mass, repro×mass	2,135	1.47	0.23	0.88	0.42

Fig. 2 Thin-plate splines displaying the relationship between log mass (*x-axis*), reproduction (*y-axis*), and log longevity (*gradations in color*) separately for herbivorous, omnivorous, and carnivorous mammals. Isoclines at given levels of log longevity were added to facilitate comparisons among figures

grades horizontally; Fig. 2). Omnivores showed an intermediate pattern with gradations in longevity along both the reproduction and mass axes. This can also be seen by comparing the slopes of the longevity isoclines among herbivores, omnivores, and carnivores (Fig. 2). Horizontal isoclines would indicate that only reproduction influences longevity, while vertical isoclines would indicate that only mass influences longevity. The slope of the longevity isoclines in herbivores is shallower than those of omnivores, especially at isoclines of 0.9 log longevity and higher. The isoclines for carnivores are the steepest, steeper than both herbivores and omnivores, and almost approach vertical (Fig. 2).

We also compared the effect of diet on reproduction (Fig. 1b). Omnivores had significantly higher reproduction than both herbivores and carnivores, which were not different from each other (ANOVA— $F_{2,470}=13.34$, $p<0.0001$; Phylogenetically controlled: default branch lengths— $F_{3,131}=3.49$, $p=0.02$, scaled branch lengths: $F_{3,131}=4.17$, $p=0.007$).

Discussion

Our results support the hypothesis that diet influences the relationship between reproduction and longevity in mammals. Reproduction is a major predictor of longevity in herbivorous mammals but much less of a predictor of longevity in carnivores. In carnivores, gradations in longevity occur strongly along the mass axis and almost perpendicular to the reproduction axis (Fig. 2). Partial correlation coefficients for the relative power of mass and reproduction to explain longevity confirm these patterns with reproduction explaining less and mass explaining more variation in longevity as trophic level increases. While the negative relationship between longevity and reproduction is considered a fundamental aspect of life history evolution (Williams 1966; Reznick 1985, 1992; Harshman and Zera 2007), relatively little is known about how this relationship varies among animals. Our results suggest that this relationship can vary

among closely related animals depending upon their trophic position.

The availability of protein in the diet may be a key factor explaining these differences. Carnivores consume food with significantly higher protein content than herbivores and protein is a key macronutrient for mammalian maintenance and reproduction, including both gestation and lactation (Speakman 2008). The higher protein content in the diet of carnivores may better allow them to simultaneously meet their protein requirements for maintenance and reproduction than herbivores. Even without conflicting nutritional demands, the protein demands of reproduction can be difficult for animals to satisfy on an herbivorous diet given the low protein content of many plants (Smith and Green 1987; Cameron and Eshelman 1996).

Less of a negative relationship between reproduction and longevity could lead to higher reproduction and/or longevity at higher trophic levels. Higher reproduction and longevity was apparent in omnivores compared to herbivores. However, there was no significant difference in reproduction or longevity between herbivores and carnivores. This suggests that there could be overall costs to carnivores that prevent them from realizing higher reproduction and longevity. One explanation is that there could be a longevity cost of high-protein diets. Focal studies of several animals have shown that, by holding total caloric content constant and varying the ratio of carbohydrates and protein or key amino acids in food, individuals fed high-protein diets have much shorter lifespans than those fed diets with less protein and more carbohydrates (Miller et al. 2005; Lee et al. 2008; Maklakov et al. 2008; Fanson et al. 2009; Simpson and Raubenheimer 2009). Changes in the concentrations of specific amino acids in the diet, especially branched-chain amino acids, could also affect longevity (Alvers et al. 2009; D'Antona et al. 2010). Another potential explanation is that, while the food that carnivores consume better allows them to avoid conflicts between reproduction and longevity, the overall availability of this food may be lower for carnivores and, hence, limit their realized reproduction and longevity. Omnivores could potentially avoid these costs by more carefully regulating their intake of protein according to their needs and consuming plant parts when animal prey are rare. Greater study of the mechanisms responsible for the unimodal relationship between diet and reproduction or longevity could provide insight into the

evolution of diet and the role of diet in aging and longevity (Simpson and Raubenheimer 2009).

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