

# PREDATOR-PREY INTERACTIONS ACROSS SCALE AND DIMENSIONALITY

*by*

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(Zoology)

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## DECLARATION

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## SUMMARY

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Predator-prey interactions are an important evolutionary driver and a central component of ecosystem structure. However, the context dependent nature of these interactions, as reflected by the diversity of species involved, means that understanding them at a fundamental level is required for purposeful predictions. In this thesis I explore the role of two fundamental components of predator-prey interactions: dimensionality and body size. I investigate the fundamental role of body size and habitat dimensionality across three chapters that represent stand-alone publications consisting of: the role of body size on the ability of species to perceive the temporal dimension of their environment; the role of habitat dimensionality and other traits relating to predation pressure on life history evolution; and the role of habitat dimensionality on the evolution of venom in snakes. Throughout my thesis I use comparative approaches to show that both habitat dimensionality and body size are key components that determine the mechanics of predator-prey interactions and hence ecological and evolutionary systems as a whole.

## PREFACE

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Several chapters from my thesis have been published elsewhere:

CHAPTER ONE has been previously published as:

**Healy K.**, McNally, L., Ruxton, G.D., Cooper, N., Jackson, A.L. 2013.

Metabolic rate and body size are linked with perception of temporal information. *Animal Behaviour*, 86, 685-696.

As lead author I was involved with the initial conception of the paper, I collected the data, designed and run the analysis and wrote the manuscript.

CHAPTER TWO has been previously published as:

**Healy K.**, Guillerme, T., Finlay, S., Kane, A., Kelly, S.B.A., McClean, D., Kelly, D.J., Donohue, I. Jackson, A.L., Cooper, N. 2014. Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc. R. Soc. B*, 281, 20140298 .

As lead author I was involved with the initial conception of the paper, lead collection and management of the data, designing and running the analysis and writing the manuscript.

**Healy K.** 2015. Eusociality but not fossoriality drives longevity in small mammals. *Proc. R. Soc. B*, 282, 20142917 .

I replied to the comment by (Williams and Shattuck, 2015) on the paper above were they show eusociality is an important factor to consider for lifespan evolution in fossorial mammals. I carried out addition analysis showing that inducing the error associated with construction phylogenies further strengthens the association between of eusociality and increased lifespan.

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## ACKNOWLEDGEMENTS

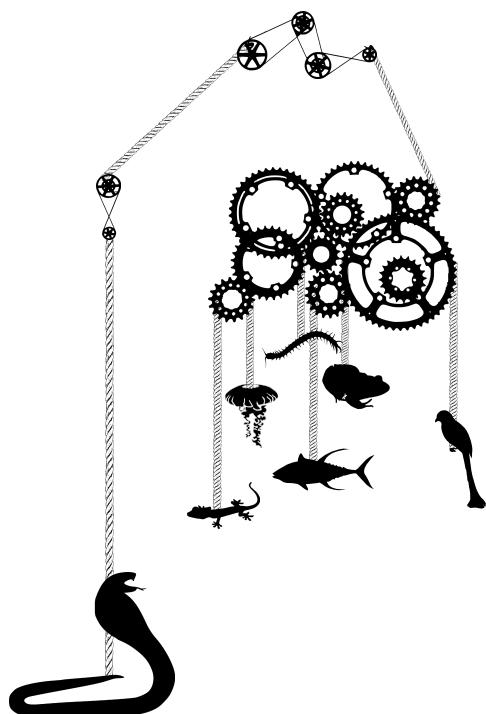
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## CHAPTER 1

# GENERAL INTRODUCTION

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“Something good”

Carl Sagan

The ability to both obtain and avoid becoming food is one of the primary selection pressures driving animal evolution. Predator-prey interactions not only shape the species directly involved but also form the fundamental building blocks of ecosystem structure, making them key to our understanding of biological systems as a whole (Pimm, 1984; Cohen et al., 1990). While these interactions are ubiquitous across diverse ecosystems each predator-prey interaction plays out within its own specific context. For example, even if hunting the same prey one predator may

rely on venom to incapacitate prey while another may rely on a strategy of high performance aerobatics to meet the same ends. However amongst these context dependencies, commonalities arise that provide a clear approach to understand how these interactions emerge and effect the systems in which they are embedded.

While the arms race between predators and their prey plays out across a diversity of forms, all players must abide to the fundamental constraints imposed by physics. For example biomechanical and physiological limitations result in flying species remaining relatively small (Chatterjee et al., 2007; Dudley, 2002) while the largest species are invariably found in the oceans (Heim et al., 2015). It is within these boundaries of physics that evolution trades off between the benefits of investing in traits relating to predator-prey interactions and the energetic costs associated with developing such traits. One common way for these trades-offs to present themselves is through there link with both body size and interaction dimensionality.

Since Kleiber fist demonstrated the link between the rate of energy utilised by an animal and its size (Kleiber, 1947) ecology has utilised this correlation to understand a range of biological processes and principles (refs). More recent formulations have attempted to use the fractal structure of physiological systems as a first principle approach to unify many aspect of biology including physiology, behaviour and ecology (West et al., 1997; Brown et al., 2004). Despite the heated debate surrounded the exact nature of this scaling and the fundamental basis that underpins it (refs summing this up), this scaling relationship has become one of the most useful proxies to many elements of biology, including predator-prey interactions (Brown et al., 2004). While body size and metabolic rate have featured as the main focus of this drive to find fundamental elements within biological complexity the dimensionality of the arena these interaction play out in has more recently gained attention as key component.

Similar to the formalisation of metabolic theory in the mid 90's the role of habitat complexity in biology has its roots in utilising the mathematics of fractals in order to explain macroecological patterns. Morse et al. (1985) was the first to utilise this geometry to describe how the space filling properties of vegetation can determine arthropod community densities through habitat availability. The the effects of habitat dimensionality was further explored in particular in primary consumers and their prey etc (see Pawar and my old thesis for refs). More recently habitat dimensionality has been re-framed as the dimensionality of the interaction between predator and prey (Pawar et al., 2012). This framework allows dimensionality to be explored

across groups and foraging strategies and extend the predictive ability of body mass scaling through the finding that high dimensional interactions have steeper scaling with body mass than expected from standard theory. It also opens up the importance of the role of sensory ecology within such interactions, in particular as such sensory systems have shown different scaling in comparison to that predicted from metabolic theory.

This thesis draws on how these two fundamental pillars of biological structure affect predator-prey interactions across the range of contexts these interactions take place. By using comparative methods I will focus on three areas; how do species sample and perceive the temporal dimension; the role of habitat dimensionality in prey species life history; and the role of habitat dimensionality in the evolution of predatory traits. By understanding the forces shaping species within the dimensions of their habitats we can gain deeper understanding of the mechanics of predator-prey interactions as a whole.

## 1.1 RESEARCH OUTLINE

### **Chapter 2: Body size, metabolic rate and visual temporal perception in vertebrates.**

All organisms must perceive the temporal dimension of their environment. This is particularly true of predators and their prey that need to accurately track and predict their adversaries' motion. Here I collate data on a measure of visual temporal perception called critical flicker fusion to test whether species that are predicted to be more maneuverable can perceive events at finer scales. I show that, as expected, small species with high metabolic rates have the fastest perception of time. This has important consequences for the ability of predators to capture their prey and I discuss some examples of adaptations in predator species that potentially mitigate against this general trend.

### **Chapter 3: Ecology and mode-of-life explain lifespan variation in birds and mammals.**

Maximum lifespan varies strongly with body mass yet many species live far longer than expected given their size. This may reflect interspecific variation in extrinsic mortality, as life-history theory predicts investment in long-term survival

when extrinsic mortality is reduced. Here, I investigate how ecological and mode-of-life traits that are predicted to reduce extrinsic mortality influence lifespan across mammals and birds. I show that species associated with high dimensional habitats, namely arboreal and volant species, show longer lifespan than expected for their body size. I discuss how habitat dimensionality may affect exposure of prey to predation pressures and the role of other ecological traits including fossoriality, eusociality, and activity patterns.

### **Chapter 4: Habitat dimensionality and a diet of eggs; the evolution of venom loss in snakes.**

Despite the obvious advantages of possessing venom there is little explanation for variation in the volume and toxicity of venom in snakes. This is particularly apparent in species that partially or fully lose the capacity to produce venom such as demonstrated in sea snake species. As venom is primarily used for capturing prey I test whether fundamental factors, including habitat dimensionality and diet, affect the amount of venom produced within a species through their influence of encounter rates and prey toxicity resistance. By collating data on venom toxicity (LD<sub>50</sub>), diets, body size, environment dimensionality and both maximum and minimum venom volumes comprising of over 75 species, I show that species found in high dimensional environments or that have egg-based diets produce less venom than their counterparts. I also demonstrate the prey-specific nature of venom toxicity using phylogenetic distance between diet species and LD<sub>50</sub> model species as a test. I discuss the possible mechanisms and the implications of these results in relation to both evolution of venom and costly predatory traits in general.

Finally, in chapter 5, I close with a discussion of the limitations of the methods used in the thesis, and suggest some future directions.

## **1.2 ADDITIONAL WORK**

In addition to the chapters enclosed in this thesis, I have also been involved in the following research during my studies:

Donohue, I., Petchey, O.L., Montoya, J.M., Jackson, A.L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N.E. & Emmerson, M.C. (2013). On the

dimensionality of ecological stability. *Ecology Letters*, 16(4), 421-429.

I was involved with the conception, data analysis and write-up of this paper.

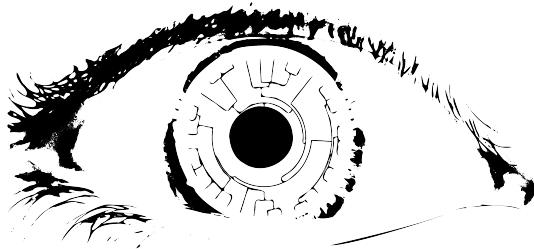
Kane, A., Ruxton, G.D., Jackson, A.L. & Healy, K.(2013). Body size drives importance of scavenging in theropods. In Review in Evolution.

I was involved with the conception, data collection and analysis, and write-up of this paper.

## CHAPTER 2

# METABOLIC RATE AND BODY SIZE ARE LINKED WITH PERCEPTION OF TEMPORAL INFORMATION

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“Time is an illusion. Lunchtime doubly so.”

Douglas Adams

### 2.1 SUMMARY

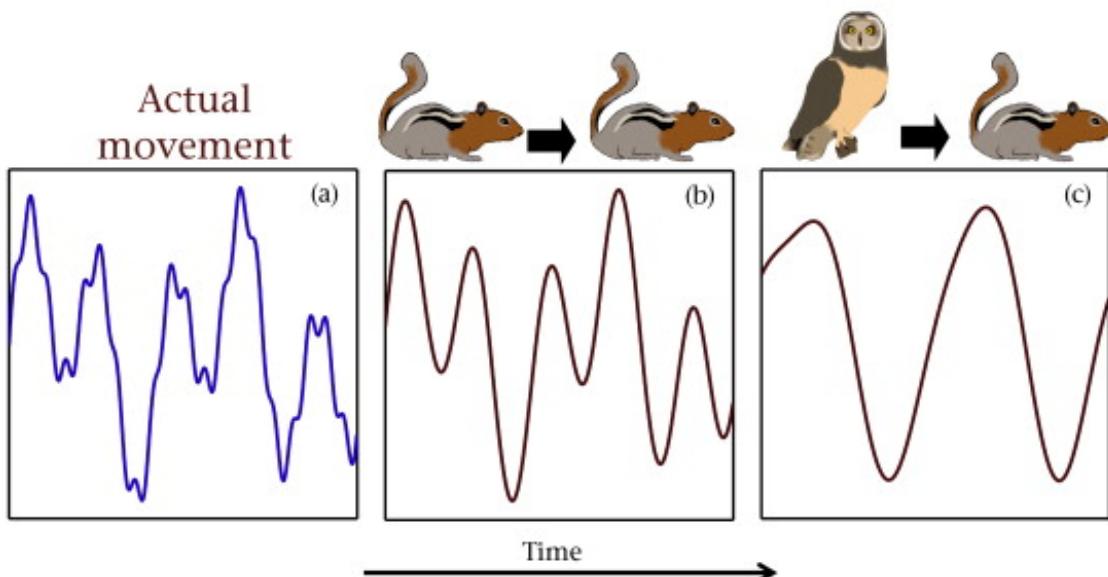
Body size and metabolic rate both fundamentally constrain how species interact with their environment. While many mechanisms leading to these constraints have been explored, their effects on the resolution at which temporal information is perceived have been largely overlooked. The visual system acts as a gateway to the dynamic environment and the relative resolution at which organisms are able to acquire and process visual information is likely to restrict their ability to interact with events around them. As both smaller size and higher metabolic rates should facilitate rapid behavioural responses these traits would be predicted to favour perception of temporal change over finer timescales. Using critical flicker fusion frequency, the lowest frequency of flashing at which a flickering light source is perceived as constant, as a measure of the maximum rate of temporal information processing in the visual system, I carry out a phylogenetic comparative analysis of a wide range of vertebrates that supports this hypothesis. These results have implications for the evolution of signalling systems and predator-prey interactions, and, combined with the strong influence that both body mass and metabolism have on a species' ecological niche, suggest that time perception may constitute an important and overlooked dimension of niche differentiation.

## 2.2 INTRODUCTION

All biological systems, from organisms to ecosystems, are shaped by universal constraints. For example, body size and metabolic rate are both known to be important determinants of organism biology, influencing life history, energetics and behaviour (Brown et al., 2004; Woodward et al., 2005; Sibly et al., 2012). More recently the fundamental role of sensory biology in ecological interactions has gained attention, such as in the limitations of target identification (Tosh and Ruxton, 2010) and the scaling allometry of sensory organs (Howland et al., 2004; Cronin, 2005; Garamszegi et al., 2002). The limitations such sensory systems are constrained by can heavily determine ecological interactions through, for example, predation and mate selection were the abilities of the parties involved to capture, escape or be seduced is dependent on how they perceive their environment (Fig. 1; Cronin 2005; Clark et al. 2012; Hornstein et al. 2000; Stevens 2007). While the ability and importance of an organism to perceive the spatial dimensions of its environments are relatively well studied (Cronin, 2005; Clark et al., 2012), how they perceive the 4<sup>th</sup> dimension, time, is less well known.

As the environment is fundamental dynamic in nature the ability to integrate information over a time period is a necessity for any organism interacting within it. Furthermore, the ability to integrate information over shorter timescales, that is, at higher resolutions, is a direct limitation on the degree to which it can interact with the environment itself. From an evolutionary perspective this leads to a trade-off between the demand for information at high temporal resolutions and the costs of its acquisition given the energetic demands associated with increased rates of neural processing in the visual system (Laughlin, 2001). This trade-off is likely to be shaped by various ecological (e.g. mode of predation) and environmental factors (e.g. light levels) as well as intrinsic factors (e.g. morphology) that will ultimately shape an organism's optimal temporal resolution for sensory perception (Autrum, 1958).

This ability to perceive and react to a dynamic environment is also likely to be an important behavioural and ecological trait. Ecologically, interaction strengths can be affected by the ability to identify and track fast-moving objects such as prey or mates (Fig. 1; Land and Collett 1974; Fritsches et al. 2005). The necessity of this ability to perceive one's environs accurately is perhaps best demonstrated in cases where temporal resolution is too coarse to allow the observer to follow the motion of a moving target accurately. A stark demonstration of this can be seen



The ability of an organism to track a moving object depends on the time integral over which the individual can obtain its information. This is determined by its ability to resolve temporal information. In cases where an animal, such as a ground squirrel, displays complex movement (a), conspecifics may perceive the individual as moving according to a first-order integral of its actual movement owing to its high temporal resolution abilities (b). However a species with lower temporal resolution abilities, such as a short-eared owl, may perceive the motion as an even higher order derivative of the actual motion, meaning information of prey motion at finer temporal scales is not available to it (c).

in the tiger beetle, *Cicindela hudsoni*, which, owing to the relatively low temporal resolution of its visual system, must take a stop-start approach in order to recalibrate the position of its prey when hunting (Gilbert, 1997). In humans, the limitations of our temporal perception are apparent when tracking fast-moving objects such as the curving trajectory of a ball in soccer (Dessing and Craig, 2010) and baseball (Bahill and Baldwin, 2004) and is also directly linked to the perception of the passage of time itself (Hagura et al., 2012).

Two intrinsic factors that may shape the costs and benefits of the temporal resolution of the sensory system, in particular with respect to their effects on an individual's ability to interact with the environment on short timescales, are body size and metabolic rate. As larger body sizes decrease manoeuvrability (Heglund and Taylor, 1988; Dudley, 2002; Biewener, 2003; Sato et al., 2007; Vogel, 2008; Hedrick, 2011; Watanabe et al., 2012) and higher metabolic rates increase both manoeuvrability and the physiological ability to process information (Li et al., 2008; Franz and Ronacher, 2002), smaller organisms and those with higher metabolic rates would be predicted to perceive temporal change on finer timescales.

To quantify the temporal perceptual abilities of a range of species I take advantage of the all or nothing nature of neural firing in the visual system. Owing to this binary firing, temporal resolution must be encoded in terms of discrete units, as biological visual systems must discretise the continuous-time and continuous-space information reaching the retina and then integrate this information over some time period. This "integration time" of visual systems can be quantified using the critical flicker fusion frequency (CFF): the lowest frequency of flashing at which a flickering light source is perceived as constant (D'EATH, 1998; Schwartz and Meese, 2010). As light intensity can increase the number of flashes that can be observed per second, the maximum CFF value, as measured in a response curve of CFF against light intensity (Ferry, 1892; Porter, 1902), can be used as a proxy for the temporal resolution of the sensory system.

Here I use maximum CFF to compare the temporal resolution of the visual system in a wide range of vertebrate species including representatives from Mammalia, Reptilia, Aves, Amphibia, Elasmobranchii and Actinopterygii. Using phylogenetic comparative methods and controlling for the light levels each species typically experiences, I test whether the temporal resolution of the sensory system increases with mass-specific metabolic rate and decreases with body mass.

## 2.3 METHODS

### 2.3.1 *Data Collection*

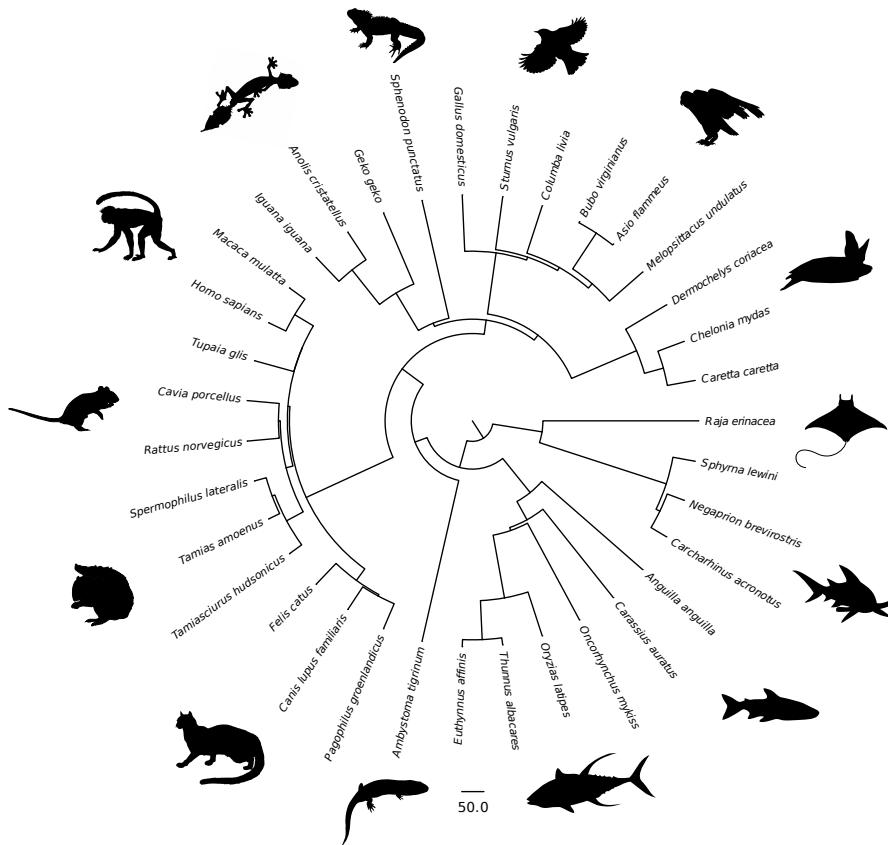
To test the prediction that CFF increases with mass-specific metabolic rate and decreases with body size (when controlling for light levels), data on maximum CFF values in vertebrate species was collated from the literature (Table 4.1). Only values from studies that measured CFF using either behavioural or electroretinogram (ERG) procedures were included. In behavioural studies, CFF is measured through conditional training with the subject trained to respond to a change in its perception of a flashing light (D'EATH, 1998; Rubene et al., 2010). For example, (Lisney et al., 2011) conducted behavioural tests in domestic chickens, *Gallus gallus*, using choice experiments with flickering and non-flickering stimuli windows with choice of the correct stimulus rewarded with food. This is repeated over a range of light intensities and flicker frequencies until individuals can no longer distinguish between the stimuli. In ERG studies, a direct measurement of the electrical response in the retina in reaction to a flashing light source is used as a measure of CFF (D'EATH,

1998; Schwartz and Meese, 2010). As there may be further processing of temporal information after it reaches the retina that may cause behavioural studies to measure lower CFF values (D'EATH, 1998), the experimental procedure used to measure CFF was included as a candidate covariate.

Mean body mass (g) published in the literature and in databases including Fish-Base (Froese and Pauly, 2012) and Animal Diversity Web (Myers et al., 2006) was collected for each species as the measure of body size. For metabolic rates mass-specific resting metabolic rate as measured by oxygen consumption through ventilation was used where the subjects were fasted prior to the measurement. These values were converted to W/g using the conversion of 20 J/ml of oxygen consumption (Makarieva et al., 2008) to allow comparison among species. For ram-ventilation species (which require constant movement to force fluid over the respiratory organs), such as sharks and tuna, the resting metabolic rate was taken as the fitted line of oxygen consumption with swimming speed extrapolated to the intercept (swimming speed = 0 m/s; 4.1). To account for the possible effect of metabolic rate measured at different temperatures in ectothermic species, metabolic rate values were corrected to 20 °C using Q10 values, i.e. the fold change in metabolic rate over a temperature change of 10 °C, for reptiles, amphibians and fish (White et al., 2006). These corrections gave values of temperature-corrected mass-specific resting metabolic rates ( $qW_g$ ), for each species. Although body mass and mass-specific metabolic rate are expected to be correlated according to an exponent of 0.25 (Brown et al., 2004; Sibly et al., 2012) (Brown et al., 2004 and Sibly et al., 2012), both terms were included as recommended by (Freckleton, 2009) instead of using residuals from a regression of body mass against mass-specific metabolic rate.

As there is a trade-off between sensitivity and movement perception owing to the requirement of longer integration times in low light conditions (Tansley et al., 1965), as is seen in the different light response dynamics of rods and cones (Rubene et al., 2010), light levels was included in the analyses as a categorical variable based on the light conditions experienced by the species during normal activity (i.e. foraging). Species were categorized as inhabiting either high or low light conditions with diurnal terrestrial and nonturbid aquatic species coded as inhabiting high light level environments and nocturnal species coded as inhabiting low light levels. As the light levels of species that inhabit turbid waters are typically orders of magnitude lower than typical daylight levels (40-1000 lx; Ali and Klyne 1985; Palmer and Grant 2010; Kreysing et al. 2012) and the harp seal, *Pagophilus groenlandicus*, regularly

forages at depths greater than 200m (Folkow et al., 2004) where light levels are comparable to nocturnal light levels (Palmer and Grant 2010), these species were categorized as inhabiting low light level environments.



Composite tree of the study species.

To correct for the phylogenetic nonindependence of species within the analysis a composite tree was constructed using published molecular phylogenies and divergence times from various sources (Schoch (1985); Jánossy (2011); Mercer and Roth (2003); Hedges et al. (2006); Wiens et al. (2006); Benton and Donoghue (2007); Murphy et al. (2007); Brown et al. (2008); Li et al. (2008); Naro-Maciel et al. (2008); Albert et al. (2009); Lim et al. (2010); Little et al. (2010); Perelman et al. (2011); see Appendix A and Figure 2.2). In instances where a divergence time was not available for two species a conservatively estimated date of first appearance was used as the divergence time taken from the Paleobiology Database (Alroy et al., 2008).

As ectotherm metabolic rates vary with temperature, a sensitivity analysis to test the effect of the temperature to which  $qW_g$  was corrected was performed by rerunning the main analysis with  $qW_g$  corrected to both  $5^{\circ}\text{C}$  and  $35^{\circ}\text{C}$  (see Appendix A). A supplemental analysis on a more restricted data set for species with available

brain mass data was also carried out to test for any possible effects of sensory tissue on maximum CFF values (see Appendix A).

In total data on maximum CFF, body mass, qWg and light environments for 34 species across the vertebrate classes Elasmobranchii, Actinopterygii, Aves, Amphiibia, Reptilia and Mammalia was collected, with further data on brain mass for 28 of these species (Table 4.1).

### 2.3.2 *Statistical Analyses*

To test the hypothesis I used a phylogenetic generalized least-squared approach (PGLS) using the caper package (Orme et al., 2011) in R version 2.14.2 (R Core Team, 2014). This approach allows for nonindependence in the data caused by species' phylogenetic relationships to be accounted for by incorporating it through the error term structure (Pagel, 1999; Rohlf, 2001). This error term consists of a matrix of expected trait covariances calculated using the maximum likelihood estimate of lambda ( $\lambda$ ), a multiplier of the off-diagonal elements of a phylogenetic variance-covariance matrix that best fits the data. When the data are structured according to a Brownian motion of trait evolution, lambda = 1, whereas when the data have no phylogenetic dependency, then lambda = 0 (Pagel, 1999).

The analysis consists of PGLS models with maximum CFF as the response variable, and all combinations of the following explanatory variables: body mass, qWg, light level (high, low) and experimental procedure (ERG, behavioural) with brain mass included in the sensitivity analysis (see Appendix A.2.2), with Akaike's information criterion (AIC) used to select the minimum adequate model (Burnham and Anderson, 2002).

## 2.4 RESULTS

The most parsimonious model (based on AIC) explaining variation in maximum CFF among vertebrates included the terms body mass, temperature-corrected mass-specific resting metabolic rate ( $qWg$ ) and light level (Table A.3). Body mass had a negative effect on the temporal resolution of the sensory system (Table A.3, Figure 2.3 a), while metabolic rate, after correcting for mass and temperature, was positively associated with CFF (Table A.3, Figure 2.3 b). Low environmental light levels were associated with an overall reduction in CFF (Table A.3, Figure 2.3). Phylogeny was found to have a minimal effect on the resulting models ( $\lambda = 0$ , Table A.3) and experimental type was not correlated with CFF (Table A.3). Thus, according to our model, small animals with high mass-specific metabolic rates in high light environments possessed the highest maximum CFF and hence greatest ability to perceive temporally dynamic visual information. Conversely, large animals with low mass-specific metabolic rates in low light environments had the lowest CFF.

These results were robust to the sensitivity analysis on both the temperature used to correct ectotherms  $qWg$  (taken as 20 °C in the main models above; see Methods) with the best models (based on AIC) including the same terms and trends as found in the main analysis (Appendix). Including brain mass in a restricted data set of 28 species for which brain mass was available did not change the effect of the explanatory variables light levels,  $qWg$  and body mass on maximum CFF (Tables A4 and A8 in the Appendix (I still need to fix these tables in the appendix up a bit)).

## 2.5 DISCUSSION

Many of the interspecific and intraspecific interactions that shape species' behaviour and ecology rely on the ability of organisms to process high temporal resolution sensory information. These results show that, while there is considerable variability in the ability to resolve temporally dynamic visual information across vertebrates, body mass and metabolic rate act as important general constraints on this ability. This is the first study to indicate a general trend in the ability of vertebrates to resolve temporal information; previous studies have generally focused on specific cases of sensory adaptations (Fritsches et al., 2005) and particular environments (Frank, 1999; Frank et al., 2012), hence focusing on the particular ecological context of each adaptation or environment. These findings illustrate the relationship between both physiology and the effects of body mass on the ability to resolve temporal

TABLE. Data used in analysis

Species	CFF	Mg	qWg	Brain Mass	Light levels
<i>Ambystoma tigrinums</i>	30 <sup>e,s,1</sup>	10.78 <sup>28</sup>	0.00016 <sup>28</sup>	NA	L
<i>Anguilla anguilla</i>	14 <sup>b,s,2</sup>	71.1 <sup>28</sup>	0.00013 <sup>28</sup>	NA	L
<i>Anolis cristatellus</i>	70 <sup>e,o,3</sup>	6.0 <sup>29</sup>	0.00089 <sup>29</sup>	NA	H
<i>Asio flammeus</i>	70 <sup>e,o,4</sup>	406.0 <sup>30</sup>	0.0032 <sup>28</sup>	5.45 <sup>69</sup>	H
<i>Bubo virginianus</i>	45 <sup>e,s,5</sup>	1450.0 <sup>31</sup>	0.0036 <sup>28</sup>	13.7 <sup>70</sup>	L
<i>Canis lupus familiaris</i>	80 <sup>b,s,6</sup>	13900.0 <sup>32</sup>	0.00183 <sup>28</sup>	80.0 <sup>71</sup>	H
<i>Carassius auratus</i>	67.2 <sup>e,o,7</sup>	10.8 <sup>33</sup>	0.00013 <sup>28</sup>	0.01 <sup>71</sup>	H
<i>Carcharhinus acronotus</i>	18 <sup>e,o,8</sup>	14491.0 <sup>8</sup>	0.00114 <sup>56*</sup>	NA	L
<i>Caretta caretta</i>	40 <sup>e,s,9</sup>	135000.0 <sup>34</sup>	0.00008 <sup>57</sup>	2.7 <sup>40</sup>	H
<i>Cavia porcellus</i>	50 <sup>e,s,10</sup>	629.0 <sup>35</sup>	0.00306 <sup>35</sup>	3.8 <sup>72</sup>	L
<i>Chelonia mydas</i>	40 <sup>e,s,9</sup>	128000.0 <sup>36</sup>	0.00025 <sup>36</sup>	8.6 <sup>71</sup>	H
<i>Columba livia</i>	100 <sup>e,s,4</sup>	315.0 <sup>37</sup>	0.0045 <sup>28</sup>	2.3 <sup>70</sup>	H
<i>Dermochelys coriacea</i>	15 <sup>e,s,11</sup>	354000.0 <sup>38</sup>	0.00043 <sup>58</sup>	30.0 <sup>73</sup>	H
<i>Felis catus</i>	55 <sup>e,s,12</sup>	3054.4 <sup>32</sup>	0.00394 <sup>59</sup>	28.4 <sup>71</sup>	L
<i>Gallus gallus domesticus</i>	87 <sup>b,o,13</sup>	2710.0 <sup>39</sup>	0.0022 <sup>28</sup>	3.6 <sup>74</sup>	H
<i>Gekko gecko</i>	20 <sup>e,s,14</sup>	54.8 <sup>40</sup>	0.00034 <sup>28</sup>	0.2 <sup>75</sup>	L
<i>Homo sapiens</i>	60 <sup>b,o,15</sup>	67100.0 <sup>41</sup>	0.00117 <sup>60</sup>	1300.0 <sup>76</sup>	H
<i>Iguana iguana</i>	80 <sup>e,s,14</sup>	750.0 <sup>42</sup>	0.00029 <sup>28</sup>	0.61 <sup>75</sup>	H
<i>Macaca mulatta</i>	95 <sup>b,o,16</sup>	7710.0 <sup>43</sup>	0.00205 <sup>61</sup>	91.7 <sup>71</sup>	H
<i>Melopsittacus undulatus</i>	74.7 <sup>b,s,17</sup>	33.6 <sup>28</sup>	0.01204 <sup>28</sup>	1.5 <sup>70</sup>	H
<i>Negaprion brevirostris</i>	37 <sup>e,s,18</sup>	92987.0 <sup>44</sup>	0.00053 <sup>62*</sup>	NA	L
<i>Oncorhynchus mykiss</i>	27 <sup>b,s,19</sup>	4000.0 <sup>45</sup>	0.00041 <sup>28</sup>	0.5 <sup>71</sup>	L
<i>Oryzias latipes</i>	37.2 <sup>e,s,20</sup>	0.21 <sup>20</sup>	0.00072 <sup>28</sup>	0.01 <sup>77</sup>	L
<i>Pagophilus groenlandicus</i>	32.7 <sup>e,s,12</sup>	119600.0 <sup>46</sup>	0.00211 <sup>63</sup>	228.5 <sup>78</sup>	L
<i>Raja erinacea</i>	30 <sup>e,o,22</sup>	500.0 <sup>47</sup>	0.00024 <sup>47</sup>	2.32 <sup>71</sup>	L
<i>Rattus norvegicus</i>	39 <sup>e,o,23</sup>	237.0 <sup>48</sup>	0.00679 <sup>48</sup>	2.3 <sup>79</sup>	L
<i>Spermophilus lateralis</i>	120 <sup>e,o,10</sup>	215.5 <sup>49</sup>	0.00335 <sup>64</sup>	3.6 <sup>80</sup>	H
<i>Sphenodon punctatus</i>	45.6 <sup>b,s,24</sup>	353.75 <sup>50</sup>	0.00017 <sup>28</sup>	NA	L
<i>Sphyrana lewini</i>	27.3 <sup>e,o,8</sup>	1893.0 <sup>8,51</sup>	0.0010 <sup>65*</sup>	60.0 <sup>77</sup>	L
<i>Sturnus vulgaris</i>	100 <sup>e,s,25</sup>	75.0 <sup>28</sup>	0.012 <sup>28</sup>	1.9 <sup>74</sup>	H
<i>Tamias amoenus</i>	100 <sup>e,o,10</sup>	51.91 <sup>52</sup>	0.00937 <sup>66</sup>	1.98 <sup>80</sup>	H
<i>Tamiasciurus hudsonicus</i>	60 <sup>e,o,10</sup>	215 <sup>35</sup>	0.00735 <sup>67</sup>	4.0 <sup>80</sup>	H
<i>Thunnus albacares</i>	80 <sup>e,s,26</sup>	45349.0 <sup>53,54</sup>	0.00158 <sup>68*</sup>	6.24 <sup>77</sup>	H
<i>Tupaia glis</i>	90 <sup>b,o,27</sup>	142.0 <sup>55</sup>	0.00424 <sup>55</sup>	3.4 <sup>79</sup>	H

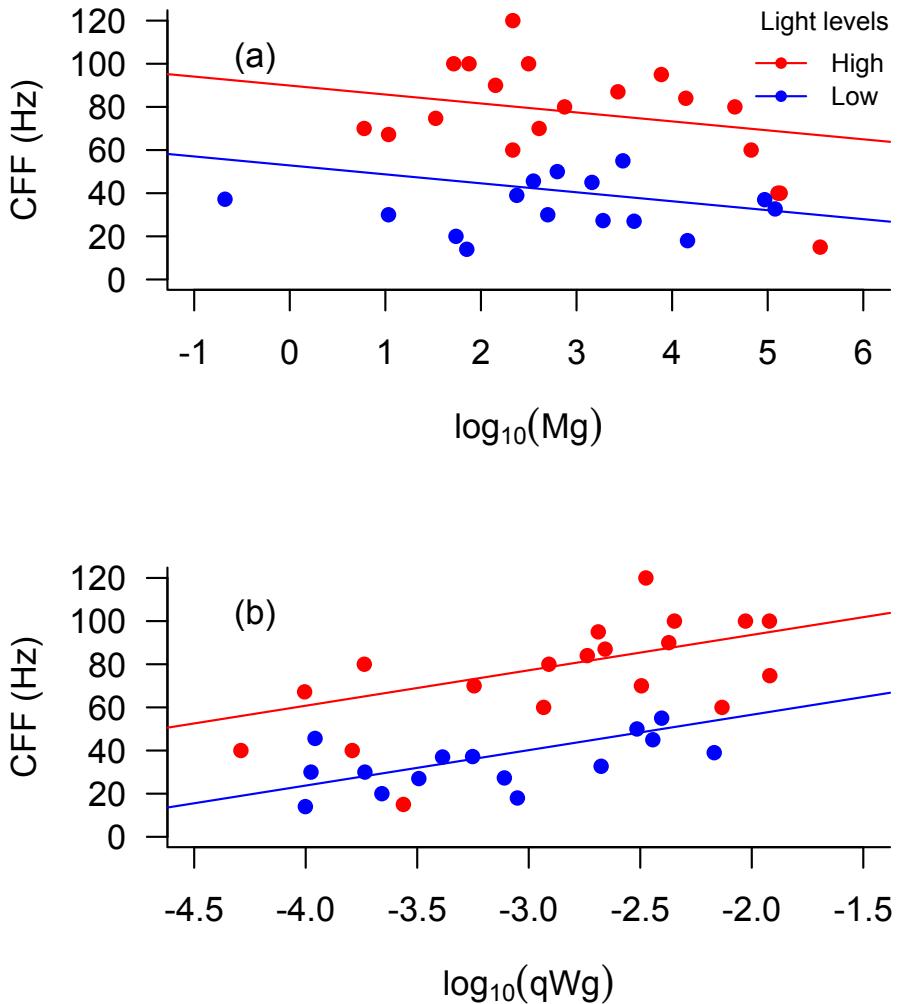
\* Indicates species with qWg estimated from swimming speeds extrapolated to zero (see Methods in main text). CFF = Critical flicker fusion (CFF), Mg = body mass (grams), qWg = Temperature corrected ( $25^{\circ}\text{C}$ ) mass specific resting metabolic rate ( $\text{Wg}^{-1}$ ), Light levels, H= High, L = Low. NA = No data available for species. Superscript indicates type of measurement, e = electroretinogram, b = behavioural experiments, o = optimum methodology, s = suboptimum methodology and numbers refer to data references; (1) Crevier & Meister (1998); (2) Adrian & Matthews (1926); (3) Fleishman et al. (1995); (4) Bornshein & Tansley (1961); (5) Ault & House (1987); (6) Coile et al. (1989); (7) Hanyu & Ali (1963); (8) McComb et al. (2010); (9) Levenson et al. (2004); (10) Tansley et al. (1961); (11) Eckert et al. (2006); (12) Loop & Berkeley (1975); (13) Lisney et al. (2011); (14) Meneghini & Hamasaki (1967); (15) Brundrett (1974); (16) Shumake et al. (1968); (17) Ginsburg & Nilsson (1971); (18) Gruber (1969); (19) Carvalho et al. (2004); (20) Carvalho et al. (2002); (21) Bernholz & Matthews (1975); (22) Green & Siegel (1975); (23) Williams et al. (1985); (24) Woo et al. (2009); (25) Greenwood et al. (2004); (26) Southwood et al. (2008); (27) Callahan & Petry (1999); (28) Makarieva et al. (2008); (29) Rogowitz (1996); (30) Gruber (1962); (31) Ganey et al. (1993); (32) Kendall et al. (1982); (33) Hughes et al. (1977); (34) Duermit (2007); (35) Arends & McNab (2001); (36) Jackson & Prange (1979); (37) Terres (1980); (38) Georges & Fossette (2006); (39) Winchester (1940); (40) Hurlburt (1996); (41) Holloway (1980); (42) Howland et al. (2004); (43) Schwartz & Kemnitz (1992); (44) Allyn (1947); (45) Ridolfi (2006); (46) Stewart & Lavigne (1984); (47) Hove & Moss (1997); (48) Hart (1971); (49) McKeever (1964); (50) Herrel et al. (2010); (51) Letourneau et al. (1998); (52) Sheppard (1968); (53) Collette & Nauen (1983); (54) Duarte-Neto & Lessa (2004); (55) Bradley & Hudson (2003); (56) Carlson (1999); (57) Lutz et al. (1989). (58) Paladino et al. (1996); (59) Eisenberg (1981); (60) Elgar & Harvey (1987); (61) Bruhn (1934); (62) Bushnell et al. (1989); (63) McNab (1986); (64) Hudson et al. (1972); (65) Lowe (2001); (66) Jones & Wang (1976); (67) Pauls (1981); (68) Dewar & Graham (1994); (69) Garamszegi et al. (2002); (70) Iwaniuk & Nelson (2002); (71)

TABLE. Coefficients of the model with all factors included. Mg = body mass (grams), qWg = Temperature corrected mass-specific resting metabolic rate Wg-1, Light.l (low) = effect of low light levels on CFF in comparison to high light levels, exp = effect of experimental type (ERG = electroretinogram) in comparison to behavior based CFF measures.

<i>Variable</i>	<i>Estimate</i>	<i>S.E</i>	<i>t-value</i>	<i>P-value</i>
Intercept	141.48	15.15	9.34	$4^{-10}$
Mg	-4.40	2.01	-2.18	0.038
qWg	16.89	4.31	3.92	$5^{-4}$
Light levels (low)	-37.74	5.94	-6.36	$7^{-7}$
Measurement type (exp)	-3.66	6.24	-0.59	0.56
Data quality (high)	-3.86	6.14	-0.63	0.53
Lambda (Low)	Mode 0	Lower 95% C.I. 0	Upper 95% C.I. 0.34	$R^2 = 0.69$

features of the environment on fine timescales, hence linking sensory adaptations to fundamental constraints and trade-offs imposed on all organisms.

The finding that metabolic rate strongly influences temporal perception extends the known influence metabolism has on organism biology. The rate at which sensory tissue can function is dependent on both the energy available and the tissues temperature. Furthermore, the rate at which neurons can transmit information is dependent on the rate at which proton pumps can re-establish a gradient potential after firing, which in turn is dependent on both metabolic rate (Laughlin, 2001) and the number of proton pumps available. It is unsurprising hence that species which have high metabolisms also benefit from an increased in the rate of sensory system functioning. In contrast species which cannot benefit from the increased rates of sensory firing are likely to reduce investment into such sensory systems, such as seems to be the case in the visual system of the deep sea escolar (Landgren et al., 2014). This is likely to partially explain the separate negative affect of body size on temporal perception as larger species in general have decreased manouevrability (Heglund and Taylor, 1988; Dudley, 2002; Biewener, 2003; Sato et al., 2007; Vogel, 2008; Hedrick, 2011; Watanabe et al., 2012) and hence less ability to react to the environment. This idea is also supported by research showing that faster and more manoeuvrable fly species have higher temporal resolutions (Laughlin and Weckström, 1993) and that less manoeuvrable scavenger crabs display slower response



The effect of log body mass, light levels and log temperature corrected mass-specific resting metabolic rate ( $qWg$ ) on critical flicker fusion frequency (CFF). The minimal adequate model (Results) indicates CFF increases with  $\log qWg$  but decreases with body mass. Low light levels (blue) are associated with low CFF values in comparison to high light levels (red).

dynamics than deeper living predatory species which are likely to have more active lifestyles (Frank et al., 2012).

While these findings establish a fundamental scaling between temporal perception, metabolism and body size many species demonstrate physiological adaptations which allow for increase sensory perception despite their size and metabolic rate. For example despite their large predatory swordfish (Fritsches et al., 2005) are capable of a ten-fold increase in their CFF, to levels expected of a small endotherm in this model. This is achieved through specialised heating tissues that increase the

temperature, and hence the metabolic rate, in their visual systems allowing them to up-regulating their CFF when hunting (Fritsches et al., 2005). Similar adaptations are also seen in other species of large, fast-swimming predatory fish (Carey, 1982; Block and Carey, 1985) and species of blowfly (Tatler et al., 2000). Physiological adaptations for high-resolution motion detection are also found within specific areas of the retina in some flies, commonly referred to as the "love spot", which allow them to identify female flight patterns accurately and thus detect mates (Land and Collett, 1974). However these species are likely to define the exception over the rule, as most species in our analysis fit well to the predict scaling.

The effects of body size and metabolic rate on temporal resolution and the presence of sensory adaptations also point towards an interesting dimension of niche space. Disparity in size and metabolic rate among species within an ecological setting may select for particular sets of adaptations creating a diverse set of sensory systems and interactions. In such a system, species might occupy the same spatial and temporal niche, but could be separated owing to differential responsiveness to environmental signals and cues as a result of having evolved divergent signalling systems along a dimension represented by temporal resolution. For example, it seems at least theoretically possible to encode information in high-frequency signals that can be detected by intended receivers such as conspecifics but that are not susceptible to "eavesdropping" by (generally larger) predators. In fact this idea has already been utilized to develop fishing lures which signal towards specify catch species yet are well camouflaged to unwanted by-catch such as marine turtles (Jordan et al., 2013; Crognale et al., 2008). Ecological systems in which this may be apparent include deep-sea systems where visual signalling is an important determinant of the ability of organisms to interact, and where bioluminescence flashing over wide frequency ranges is ubiquitous (Haddock et al., 2005; Widder, 2010). Similarly urban lighting may also create such variation in perceptual space for species with possible negative affects on species with high temporal perceptions as the flickering rate of street light may both reduce the advantages such species have over their prey or cause increased stress such as observed in birds species kept in captivity (Inger et al., 2014).

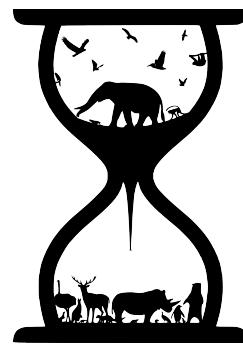
Overall these results show that not only are body size and metabolic rate good proxies for the rate of biological interactions they are good proxies for the ability to perceive such interactions. While interaction rates are strongly coupled with the spatial dimensionality of the environment and searching rates associated with them

(Pawar et al., 2012) the temporal dimension in which an individual resides will also strongly influence its ability to interact with that environment. The generality of these findings suggest that temporal resolution may play a much more important role in sensory ecology than previously indicated, in particular because of its universal effects relating to body size. Further investigations into both the underlying mechanisms of these findings and their importance to ecological functioning are needed.

## CHAPTER 3

# ECOLOGY AND MODE-OF-LIFE EXPLAIN LIFESPAN VARIATION IN BIRDS AND MAMMALS

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“Achieving life is not the equivalent of avoiding death.”

Ayn Rand

### 3.1 SUMMARY

Many species live far longer than expected given their body mass. This may reflect interspecific variation in extrinsic mortality, with species capable of reducing mortality expected to exhibit longer lifespans. One such factor that may strongly influence such extrinsic mortality is habitat dimensionality. As higher dimensional habitats create multiple escape routes from predation, species associated with such environments would be expected to have higher maximum lifespans. Here, I investigate how such traits associated with habitat dimensionality inducing volancy, arboreality and fossoriality, along with other potential traits, including activity patterns and eusociality, influence lifespan across birds and mammals. Using phylogenetic comparative analyses with over 1300 species I show that, over and above the effect of body mass, species associated with high dimensional habitats, through arboreality and the ability to fly, live the longest. Within volant species, lifespan depended upon when (activity patterns), but not where (foraging habitats), species are active. However, the opposite was true for non-volant species, where lifespan correlated positively

with both arboreality and whether they were eusocial. These results indicate that dimensionality can affect the ability of prey to escape predation with the resulting affects on species life-history evolution.

### 3.2 INTRODUCTION

Lifespan, or longevity, is a fundamental life-history trait that exhibits considerable variation both within and among species. Maximum lifespan in vertebrates, for example, ranges from up to 211 years in the bowhead whale (*Balaena mysticetus*;(De Magalhaes and Costa, 2009)), down to just eight weeks in the pygmy goby (*Eviota sigillata*; (Depczynski and Bellwood, 2005)). Like most other life-history traits, lifespan varies strongly with body size such that large species tend to live longer than smaller species (Lindstedt and Calder III, 1981; Promislow, 1993; De Magalhães et al., 2007; Ricklefs, 2010b). However, many species have far longer, or indeed shorter, lives than expected given their body mass (Figure 3.1)). Understanding the mechanisms underlying these deviations from predicted lifespan may reveal the secrets to treating and combating human ageing (Ricklefs, 2010a; Zhang et al., 2013).

One explanation for species living longer than expected, given their body size, is that low extrinsic mortality (i.e. low risk of death due to external causes such as disease, predation, food shortages or accidents) will, on average, select for longer lifespans than when extrinsic mortality is high (Stearns, 1992; Williams, 1957). This is because when untimely death is more likely, investment in early and frequent reproduction is favoured rather than investment in long-term maintenance and survival. Therefore, species with adaptations that reduce the risks of extrinsic mortality should live longer than expected, given their body mass (Partridge and Barton, 1993). These ideas have led to myriad, taxon-specific hypotheses about traits that may reduce extrinsic mortality and result in increased lifespan (Ricklefs, 2010a). However, there is little consensus about the general drivers of increased lifespan across clades.

As predation is one of the main sources of extrinsic mortality, species which possess the ability to reduce it, for example through the use of toxin defences, show increased lifespans (Hossie et al., 2013). One fundamental ecological aspect that would be expected to affect such predation pressures is the dimensionality of the habitat a species lives within. The dimensionality of trophic interactions is a key

element in predation pressures where consumption rates scale higher with body mass in high dimensional interactions (Pawar et al., 2012). While this increased scaling of potential predation pressures may be expected to decrease prey species longevity in such environments the converse may also be expected through the increase ability of prey species to escape due to the increased availability of escape routes in terms of directionality and cover (Møller, 2010). Two common ways a species may access such escape paths are arboreality and the ability to fly.

The ability to fly, and thus more easily escape predation and unfavourable conditions, is perhaps the most effective way a terrestrial species can evolve to reduce its extrinsic mortality and increase its lifespan (Partridge and Barton, 1993; Holmes and Austad, 1994; Pomeroy, 1990). This is supported strongly by striking differences in the lifespan of volant (flying) and non-volant (non-flying) vertebrates; on average, bats live 3.5 times longer than similarly-sized non-volant placental mammals (Wilkinson and South, 2002; Austad and Fischer, 1991), while birds live up to four times longer than similarly sized mammals (Lindstedt and Calder III, 1981; Holmes and Ottinger, 2003). Similarly arboreality has also been cited as extending longevity in species mainly through decreasing predations risks (Shattuck and Williams, 2010). However, these may not be the only route to reducing extrinsic mortality and thereby increase lifespan. Ecological factors may also be important. Previous studies have investigated the relationship between lifespan and various ecological variables, but most only investigated select groups of species and few considered multiple traits simultaneously (e.g. Shattuck and Williams (2010)).

Here I investigate how multiple ecological and mode-of-life traits simultaneously influence maximum lifespan across birds and mammals. I test several hypothesis regarding the relationships among lifespan and ecological and mode-of-life traits known to influence extrinsic mortality risk; including flight capability (volant or non-volant), activity period (diurnal, crepuscular [i.e. active at dawn and dusk], nocturnal or cathemeral [i.e. active both day and night]), foraging environment (terrestrial, semi-arboreal, arboreal, aerial or aquatic), and fossoriality (i.e. living in burrows; fossorial, semi-fossorial, non-fossorial). I approach these questions by using the largest number of species to date in such an analysis ( $N = 589$  birds and 779 mammals) and by using the most up to date phylogenetic comparative approach that includes using a distribution of 500 combined bird and mammal phylogenies to control for the phylogenetic autocorrelation introduced by shared ancestry (Harvey and Pagel, 1991) and body mass (Lindstedt and Calder III, 1981).

I predict that, after controlling for body mass, (i) species which can access escape routes within high dimensional habitats including volant and arboreal species will either show reduced or enhanced lifespans in comparison to other species; (ii) semi-arbooreal, semi-aquatic and semi-fossorial species which can seek refuge across different environments would be expected to live longer than terrestrial species; species with nocturnal, crepuscular or cathemeral activity patterns will live longer than diurnal species, because species that are active at night or dusk are likely to be harder for predators to detect (Holmes and Austad, 1994; Promislow and Harvey, 1990); and (4) fossorial (i.e. species that live in permanent burrows) will live longer than purely terrestrial species, because they possess means to escape predation and unfavourable conditions through refuge (Buffenstein and Jarvis, 2002).

As ecological factors that influence lifespan are likely to vary among volant and non-volant species because sources of extrinsic mortality will differ in these two groups, these groups were split species into volant (most birds and all bats), and non-volant (some birds and most mammals) subgroups, to discover general, broad-scale correlates of lifespan in endotherms, rather than separate correlates for birds and mammals. I then tested the above hypotheses on volant and non-volant species separately. As predicted, after controlling for body mass and phylogeny, volant and arboreal species live longer than terrestrial species. Surprisingly of the species capable of transitioning across environments only semi-arbooreal species showed increased lifespan while only volant crepuscular species showed any effect of activity period on longevity.

### 3.3 MATERIALS AND METHODS

#### 3.3.1 *Data*

I used maximum longevity as a measure of lifespan as it is thought to be the best available estimator of a species' ageing rate (De Magalhães et al., 2007) and because of the amount of high quality longevity data available. Data on maximum longevity (years) and adult body mass (g) was obtained from the AnAge database (De Magalhaes and Costa, 2009; Tacutu et al., 2012). In the main analysis species with maximum longevity estimates based on fewer than ten longevity records, or with low or questionable data quality as defined in the AnAge database were excluded (De Magalhães et al., 2007). As maximum values are dependent on sample size a sensitivity analysis excluding species with maximum longevity estimated from fewer

than 100 longevity records we also run. Note that longevity records for non-volant mammals tend to come from captive individuals, whereas data for bats and birds tend to come from wild caught individuals. Although we expect captive individuals to live longer than wild individuals, on average maximum longevity tends to remain unchanged between captive and wild populations Ricklefs and Scheuerlein (2001). Further, given that bats and birds live longer than non-volant mammals, this should make the analyses more conservative.

To test the hypotheses concerning the relationships between lifespan, mode-of-life and ecological traits, data was collected on the flight capability (volant or non-volant), activity period (diurnal, crepuscular, nocturnal or cathemeral), foraging environment (terrestrial, semi-arboreal, arboreal, aerial or aquatic), and fossoriality (fossorial, semi-fossorial or non-fossorial) of each species using Walker's Mammals of the World (Nowak, 1999), the Handbook of Birds of the World series (Hoyo et al., 1992), the Handbook of the Birds of Europe, the Middle East and North Africa series (Cramp, 1977) and some additional sources (Appendix B, (Fry and Fry, 2010; Parr and Juniper, 2010; Williams et al., 1995)). I used the taxonomy of Wilson and Reeder (Wilson and Reeder, 2005) for mammals and Jetz et al. Jetz et al. (2012) for birds and excluded purely aquatic mammals (Cetacea and Sirenia) from the analyses because we expect selection pressures to be very different in these groups. Gliding mammals were also excluded because there were too few species ( $N = 9$ ) to run a separate analysis and because this group could equally fit into either the volant or non-volant subgroups.

Rather than basing the analyses on just a single phylogenetic tree and assuming this tree was known without error, a distribution of trees was used. For birds 500 trees were extracted from the posterior distribution of a recent bird phylogeny generated under a Bayesian inference framework (Jetz et al., 2012), and for mammals the 10,000 mammal trees constructed by Kuhn et al. (2011) was used. Each individual mammal tree comprises one resolution of the polytomies of a previously published supertree (Bininda-Emonds et al., 2007). These were treated as equivalent to a Bayesian posterior distribution of trees because no such tree analysis exists for all mammals. To create a distribution of phylogenies containing both birds and mammals, randomly selected bird tree and mammal trees were selected without replacement and bound to make a combined tree. The trees were bound with a root age of 315 million years, corresponding to the fossil calibration for all amniotes, i.e., *Archerpeton anthracos* (Appendix B; (Reisz and Müller, 2004)). This procedure was

repeated 500 times to generate a distribution of 500 combined bird and mammal trees.

In total the analyses used data from 589 birds (579 volant and 10 non-volant) and 779 mammals (83 volant and 696 non-volant; see Appendix B: Table A1 for more details), which was reduced to 474 birds and 435 mammals in the sensitivity analysis using only species with 100 or more longevity records.

### 3.3.2 Analyses

To test the hypotheses the following three models were fitted, with Maximum longevity and Body mass incorporated as continuous variables; Flight capability, Foraging environment, Activity period and Fossoriality as factors and with Body mass:Flight capability representing the interaction between Body mass and Flight capability:

1. For all species (N =1368: Maximum longevity =  $f(\text{Body mass} + \text{Flight capability} + \text{Body mass: Flight capability})$ )
2. For volant species only (N = 662): Maximum longevity =  $f(\text{Body mass} + \text{Foraging environment} + \text{Activity period})$
3. For non-volant species only (N =706): Maximum longevity =  $f(\text{Body mass} + \text{Foraging environment} + \text{Fossoriality} + \text{Activity period})$

All analyses were carried out in R v3.0.2 (R Core Team, 2014). Maximum longevity and body mass were  $\log_{10}$  transformed before being mean centred and expressed in units of standard deviation. The models were fitted using Bayesian phylogenetic mixed models from the MCMCglmm package (Hadfield et al., 2010), to account for non-independence in species traits introduced as a result of common ancestry (Harvey and Pagel, 1991). MCMCglmm uses a Markov chain Monte Carlo estimation approach and accounts for non-independence among closely-related species by including the phylogenetic relationships among species as a random variable. I determined the number of iterations, thinning and the burn-in period for each model run across all trees using diagnostics in the coda package (Plummer et al., 2006) and checked for convergence between model chains using the Gelman-Rubin statistic, the potential scale reduction factor (PSR), with all models required have a PSR below 1.1 (Gelman and Rubin, 1992). Following the recommendations of Hadfield (Hadfield et al., 2010), an uninformative inverse-Wishart distribution (with variance, V, set to 0.5 and belief parameter, nu, set to 0.002) and a parameter

expanded prior, with a half-Cauchy distribution (described by the parameters  $V = 0.5$ ,  $\text{nu} = 1$ , the prior mean  $\text{alpha.mu} = 0$ , and  $\text{alpha.V} = 102$ , which represents the prior standard deviation with a scale of 10), was used for the random factor to improve mixing and decrease autocorrelation among iterations.

As noted above, rather than using one phylogenetic tree and assuming this tree was error free, a distribution of 500 combined bird and mammal trees was used with each of the models fitted to each of these trees. The resulting model outputs were then combined to give model estimates which incorporate the error across the 500 trees. As the posterior outputs of MCMC models are combinable, coefficient distributions were created by amalgamating each coefficient posterior.

To determine whether the conclusions held when species with fewer than 100 longevity records was excluded, models 1-3 were repeated with the reduced dataset of species with 100 or more longevity records. I also repeated Models 2 and 3 for birds and mammals (rather than volant and non-volant species) separately to ensure that differences between the volant and non-volant subgroups were due to differences in flight capability and were not simply representing the difference between mammals and birds. The deviance information criteria (DIC), a hierachal generalization of AIC, was calculated for each paired bird and mammal models and compared to the paired volant and non-volant models of the same phylogeny to compare model "fit" of each approach.

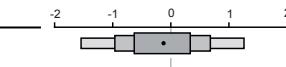
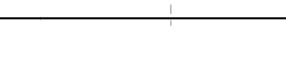
Finally, Since publication of this work (Healy et al., 2014) new analysis performed by Williams and Shattuck (2015) outlined the potential importance of eusociality in small mammals associated with fossoriality. The analysis uses the data described above along with new data on eusociality, defined using reproductive skew (Williams and Shattuck, 2015), to show that eusociality is also a predictor of increased maximum lifespans. To further investigate the role of eusociality using the methods developed here I run a further analysis on this composite dataset to control for both phylogeny and the error within phylogenetic reconstructions.

### 3.4 RESULTS

The analysis show that volant species live longer than non-volant species of a similar body mass (Table 1, Figure 1). In addition, for a given increase in body mass, the lifespans of volant species (modal slope estimate [after converting from mean-centred values] = 0.25; Table 1) increase significantly more than the lifespans of non-

volant species (modal slope estimate [after converting from mean-centred values] = 0.13; Table 1).

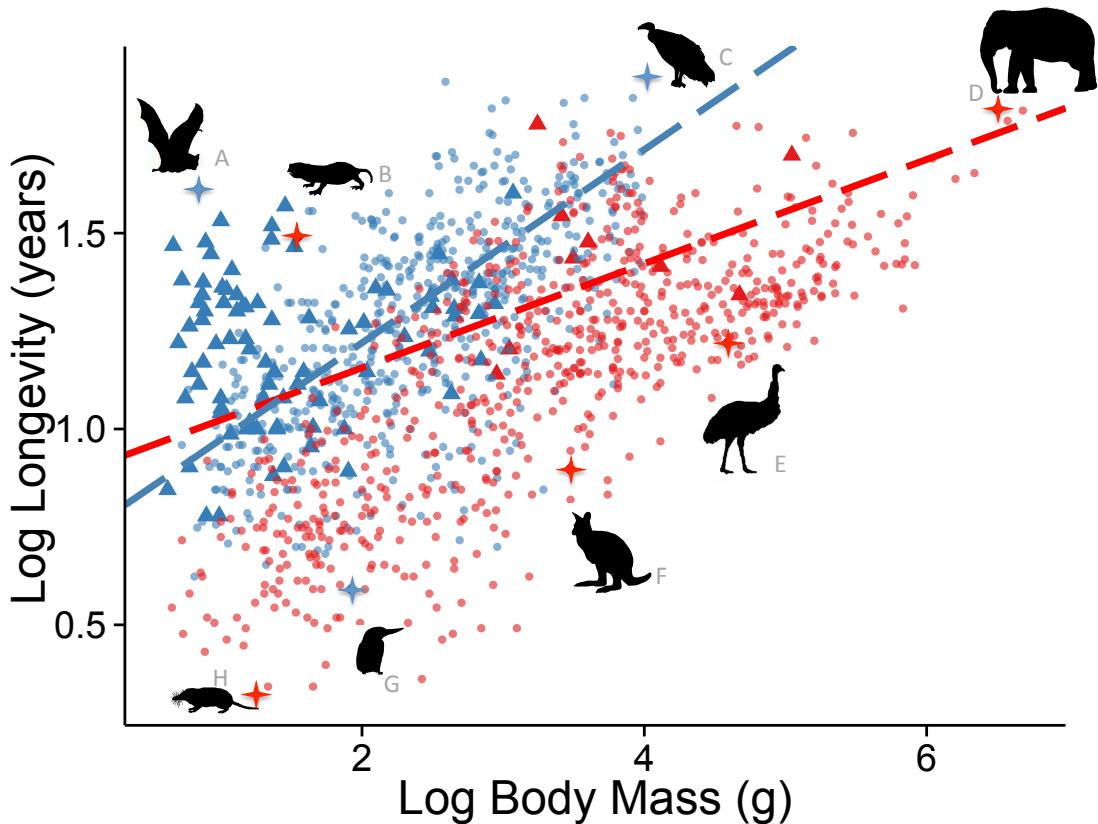
TABLE. Relationship between maximum longevity (years), body mass (g) and flight capability (volant or non-volant) in 1368 birds and mammals. Estimates are modal estimates from 500 models. Lower CI = Lower 95% confidence interval from 500 models. Upper CI = Upper 95% confidence interval from 500 models. Posterior distribution = distribution of estimates from 500 models. Body mass × Flight capability = interaction between body mass and flight capability.

Fixed Terms	Estimate ( $\beta$ )	Lower CI	Upper CI	Posterior distribution
Intercept	-0.145	-1.544	1.260	
Body Mass	0.554	0.467	0.639	
Flight capability - Volant	0.507	0.033	0.981	
Body Mass: Flight capability	0.456	0.302	0.613	
<hr/>				
Random Terms				
Residual variance	0.107	0.090	0.127	
Phylogenetic variance	1.542	1.264	1.871	

Notes: 24000000 iterations with 4000000 burnin and thinning interval of 10000.

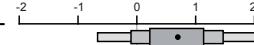
The relationships among our ecological variables and lifespan differed between the volant and non-volant subgroups. Within volant taxa, crepuscular species (i.e. those active at dusk and dawn) had significantly shorter lifespans than both diurnal and nocturnal species (Table 2). In contrast, activity period was not associated with lifespan in non-volant species (Table 3). Foraging environment did not influence lifespan significantly in volant species; bats and birds that forage on the ground do not have shorter lifespans than species that forage in the air or in trees (Table 2). Within non-volant species, however, those foraging arboreally have longer lifespans than those foraging terrestrially, and fossorial (i.e. burrowing) species live longer than non-fossorial ones (Table 3).

In the supplementary analysis with maximum longevity estimates based on 100 or more records, the models showed qualitatively comparable results to the findings in the main analysis (Appendix B: Tables B2-B4). In the repeated Models 2 and 3 for birds and mammals (rather than volant and non-volant species), the results were qualitatively identical apart from a predictable reduction in the phylogenetic residual term and also a lower combined DIC value for Models 2 and 3 (modal volant and non-volant DIC = 1184) in comparison to a taxonomically split model (modal birds and mammals DIC = 1227) (Appendix B: Tables B5-B6). The phylogenetic residual term was high in all of our models (model 1: 1.542; model 2: 1.555; model 3: 1.627;



Relationships between body mass and maximum lifespan in birds and mammals. Silhouettes highlight a selection of species with much longer or shorter lifespans than expected given their body size. These species are (A) *Myotis brandtii*, Brandt's bat; (B) *Heterocephalus glaber*, Naked mole rat; (C) *Vultur gryphus*, Andean condor; (D) *Loxodonta Africana*, African elephant; (E) *Dromaius novaehollandiae*, Emu; (F) *Dorcopsulus macleayi*, Papuan forest-wallaby; (G) *Ceryle rudis*, Pied kingfisher; and (H) *Myosorex varius*, Forest shrew. Blue points and line represent volant birds and mammals ( $N = 662$ ; slope = 0.25, intercept = 0.73). Red points and line represent non-volant birds and mammals ( $N = 706$ ; slope = 0.13, intercept = 0.89). Blue triangles represent bat species and red triangles represent non-volant bird species. Estimates of slopes and intercepts represent back transformed values from mean centred values given in Table 1.

TABLE. Relationship between maximum longevity (years), body mass (g), foraging environment and activity period in 662 volant birds and mammals. Estimates are modal estimates from 500 models. Lower CI = Lower 95% confidence interval from 500 models. Upper CI = Upper 95% confidence interval from 500 models. Posterior distribution = distribution of estimates from 500 models.

Fixed Terms	Estimate ( $\beta$ )	Lower CI	Upper CI	Posterior distribution
<b>Intercept</b>	0.668	-0.664	2.028	
<b>Body Mass</b>	1.035	0.899	1.172	
<b>Foraging environment</b>	- Aerial	0.116	-0.119	
	- Arboreal	0.068	-0.119	
	- Semi-arboreal	0.124	-0.056	
	- Aquatic	-0.166	-0.383	
<b>Activity period</b>	- Cathemeral	0.085	-0.088	
	- Crepuscular	-0.479	-0.772	
	- Nocturnal	-0.131	-0.385	
<hr/>				
<b>Random Terms</b>				
<b>Residual variance</b>	0.184	0.151	0.223	
<b>Phylogenetic variance</b>	1.155	0.789	1.693	

Notes: 12000000 iterations with 2000000 burnin and thinning interval of 5000.

Tables 1-3) but was much lower in the taxonomically split bird and mammal models, as expected given their more restricted phylogenetic scope (birds: 0.371; mammals: 0.936; Appendix 3, Table A10). Finally, the additional analysis of Williams and Shattuck (2015) dataset showed that eusociality but not fossoriality (as defined to include both semi-fossorial and fully fossorial species) increased maximum lifespan in small mammals. (Table 4).

### 3.5 DISCUSSION

As predicted, these analysis found that species capable of exploiting high dimensional environments live longer than species of a similar body mass in environments of lower dimensionality. Volant species, in particular those with nocturnal, cathemeral and diurnal activity patterns, lived longer than non-volant species while the longest-lived non-volant species tended to be arboreal or semi-arboreal. The link between these traits and increased lifespan are in line with previous studies on lifespan evolution in endotherms. Among birds, flightless or weakly-flying species (i.e. game birds) have the shortest lifespans (Ricklefs, 2010b; Williams, 1957; Wilkinson and

TABLE. Relationship between maximum longevity (years), body mass (g), foraging environment, fossoriality and activity period in 706 non-volant birds and mammals. Estimates are modal estimates from 500 models. Lower CI = Lower 95% confidence interval from 500 models. Upper CI = Upper 95% confidence interval from 500 models. Posterior distribution = distribution of estimates from 500 models.

Fixed Terms	Estimate ( $\beta$ )	Lower CI	Upper CI	Posterior distribution
<b>Intercept</b>	0.013	-1.433	1.467	
<b>Body Mass</b>	0.531	0.449	0.614	
<b>Foraging environment</b>	- Arboreal	0.213	0.358	
	- Semi-arboreal	0.148	0.274	
	- Aquatic	0.064	0.341	
<b>Fossoriality</b>	- Fossorial	0.437	0.785	
	- Semi-fossorial	0.035	0.149	
<b>Activity period</b>	- Cathemeral	0.060	0.173	
	- Crepuscular	-0.050	0.096	
	- Nocturnal	0.038	0.153	
<b>Random Terms</b>				
<b>Residual variance</b>	0.042	0.031	0.059	
<b>Phylogenetic variance</b>	1.627	1.319	1.985	

Notes: 24000000 iterations with 4000000 burnin and thinning interval of 10000.

TABLE. Relationship between maximum longevity (months), body mass (g), sociality (eusocial or no-eusocial) and fossoriality (fossorial non-fossorial). Estimates are modal estimates from 25 models. Lower CI = Lower 95% confidence interval from 25 models. Upper CI = Upper 95% confidence interval from 25 models. Posterior distribution = distribution of estimates from 25 models.

Fixed Terms	Estimate ( $\beta$ )	Lower CI	Upper CI	Posterior distribution
<b>Intercept</b>	0.552	-0.410	1.546	
<b>Body Mass</b>	0.534	0.383	0.683	
<b>Sociality: Eusocial</b>	0.289	0.070	0.511	
<b>Habitat: Fossorial</b>	0.064	-0.175	0.129	
<b>Random Terms</b>				
<b>Phylogenetic variance</b>	1.002	0.635	1.420	
<b>Residual variance</b>	0.064	0.036	0.103	

Notes: 5100000 iterations with 100000 burnin and thinning interval of 2500.

South, 2002) while among mammals, bats live far longer than similarly sized non-volant mammals (ref). Arboreality is also strongly associated with longer lifespans (Shattuck and Williams, 2010) while gliding species, which mix elements of both

arboreality and volancy, also have greater lifespans than expected given their body mass (Holmes and Austad, 1994). This increased lifespan is likely associated with the decreased predation pressures associated with living within high dimensional environments.

High dimensional environments may reduce predation risks through providing refuge that predators cannot access and through providing more escape routes in terms of directionality. Prey escape strategies often involve retreating to a refuge that cannot be accessed by the predator in pursuit, such as transiting between terrestrial, arbooreal, aquatic or fossorial environments. However the results off this analysis suggest that this is not a major contributor to lifespan evolution in endotherms as semi-aquatic and semi-fossorial species show no difference in longevity in comparison to fully terrestrial species. The increased longevity in higher dimensional environments may hence better reflect the increased options available for escape in such habitats. In fact birds species that escape along vertical flight trajectory's (3D) have been found to have longer lifespans in comparison to those that use horizontal escape routes (Møller, 2010).

Another explanation for these results of increased lifespan in volant and arboreal species is that the environments included within this analysis restrict large predators. Unlike marine environments aerial and arboreal environments severely restrict body size, mainly through biomechanical constraints. This is seen in the largest known aerial predators, *Argentavis*, reaching only 70 kg (Chatterjee et al., 2007) whereas the largest extant terrestrial predators can reach up to 1000 kg (Carwardine, 1995), while the largest extinct theropods species reach over 15 tonnes (Therrien and Henderson, 2007). Similarly arboreal predators are restricted by the weight branches can support with the largest such predators, felids, generally restricted to ticker branches. This exclusion of large body size species may also explain the difference in how lifespan scaled with body mass found in volant and non-volant species. While previous studies generated similar slopes for the relationship between log lifespan and log body mass in birds (slope = 0.20) and mammals (slope = 0.22) (Lindstedt and Calder III, 1981; Hulbert et al., 2007) these analysis show for a given increase in body mass, the lifespans of volant species (modal slope estimate [after converting from mean-centred values] = 0.25) increase significantly more than the lifespans of non-volant species (modal slope estimate [after converting from mean-centred values] = 0.13). This difference in scaling may reflect the relativity predator free existence of large flying species such as found in species of vultures and albatross.

While habitat dimensionality shows an important effect on longevity, activity patterns in both volant and non-volant species seems to show little association with lifespan. Only crepuscularity in volant species showed an effect with these species having shorter maximum lifespans. This may be a result of crepuscular species being exposed to both diurnal and nocturnal predators resulting in higher extrinsic mortality. For example bat species which emerge earliest are susceptible to the highest predation levels (Jones and Rydell, 1994). The scarcity of crepuscular volant species ( $N = 16$ ) in our dataset also suggests that specialisation to be active between nocturnal and diurnal periods is a relatively unsuccessful strategy. Activity period was not related to lifespan in non-volant species, counter to the initial prediction that nocturnal, crepuscular and cathemeral species would be more long-lived, which assumed that diurnal species would be easier for predators to detect. However, there are many additional ways to avoid predation and many alternative reasons for becoming nocturnal, crepuscular or cathemeral. For example, many large mammals are crepuscular or cathemeral in order to avoid the intense heat of the day in tropical areas, while species such as wolves and hyenas may have become nocturnal to access more prey. Consequently, although nocturnality may decrease extrinsic mortality for some species, it may actually increase it for others Prugh and Golden (2014).

Within the main analysis fully fossorial species lived longer than similar sized terrestrial species, as expected based on the inferred protection such a lifestyle may provide against predators. However subsequent analysis here, following Williams and Shattuck (2015), showed that this association is more likely to be driven by the levels of eusociality found in fossorial species. Eusociality is also known to increase longevity through the reduce extrinsic mortality in breeding individuals. For example eusocial insects, perhaps the most extreme example of such systems, show a 100-fold increase in maximum lifespan in the colony queens (Keller and Genoud, 1997). Of the 10 fully fossorial species included in our original analysis the three species which can be best described as eusocial, the naked mole rats *Heterocephalus glaber*; *Cryptomys damarensis*; *Spalax ehrenbergi* have maximum lifespans ranging between 15.5 and 32 years in comparison to the range of 2.5-17 years in the remaining fossorial species. This new analysis suggest that fossoriality itself does not confer additional protection from external mortality. This may be due to fossoriality restricting the means of escape once encountered by a predator within the borrow. Hence this result further supports the idea that dimensionality

is an important aspect of reducing mortality and may offer a partial explanation for the exceptional longevity of naked mole rats (*Heterocephalus glaber*) which live ten times longer than expected, given their body size (Buffenstein and Jarvis, 2002).

These findings highlight the potential importance of habitat complexity in lifespan evolution. The additional options for escape in such habitats may be a defining feature of trophic interactions within birds and mammals. However the biomechanical limitations associated with volancy and arboREALITY, restrict the ability to draw out whether this is the causal factor behind such increased lifespans. Further comparative analysis in marine systems where such body size limitations are less restrictive and where pelagic systems are relatively clear of refuges would provide a further test to the above conclusions. In particular if habitat dimensionality is an important factor in lifespan evolution it would be expected that pelagic species live longer than similar sized benthic species while accounting for phylogeny. Similarly other groups may help further decouple the effects of fossoriality on life history evolution. In particular comparing the diverse ecologies within reptiles would further test the effects of arboreality and fossoriality on lifespan.

Finally, while the ability to escape some of the main sources of mortality is likely to extend species lifespan and the associations between longevity and volancy, arboreality and eusociality is clear the direct causal link is still not clear. Theoretical modelling suggests that how mortality is distributed across a species demography is a key determinant in whether that species increases its lifespan. For example reduced extrinsic mortality, especially due to predation, may increase intraspecific competition resulting in what seems as a counter-intuitive reduction in lifespan (Moorad and Promislow, 2010). To decouple such effects more detailed analysis including mortality rates across species life-histories along with comparative methods which include ecology are needed. By understanding the underpinnings of the evolution of life-history we not only provide an insight into the ecology and evolution of predator-prey interactions but also provide an important basis on which to view and understand our own ageing and the potential paths to circumvent it.

## CHAPTER 4

# HABITAT DIMENSIONALITY AND A DIET OF EGGS: THE EVOLUTION OF VENOM LOSS IN SNAKES.

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“Round and round they went with their snakes, snakily...”

Aldous Huxley

### 4.1 SUMMARY

The evolution of venom in snakes offers a system of ecological, evolutionary and medical interest. Despite this many fundamental questions regarding the evolution and variation of this trait amongst snakes still persist, such as the perplexing range in the toxicity and quantities venom across species. For example despite the obvious benefits of possessing venom many species have secondarily either lost or severely reduced the toxicity or volume of venom produced. One of the potential answers to this paradox is the reduction of costs associated with producing large amounts of venom in species where the benefits of venom are reduced. Here I test several hypothesis on such ecological factors that may be associated with the atrophy of venom in snakes including habitat dimensionality, which is predicted to

affect encounter rates, diet and body size. Further to this I test the co-evolutionary relationship between venom toxicity and venom volume along with the levels of prey-specificity in a comparative analysis using over 100 species of venomous snakes. I find that species with associations to high dimensional habitats and a diet of eggs show atrophy of venom through reduced venom volumes and in the case of eggs eating reduced toxicity. These results also show that, despite predictions, levels of toxicity show no association with the volume of venom produced. However snake venom was found to be prey-specific with venoms tested on models closely related to the diets of that species showing higher levels of toxicity. Overall snake venom provides a remarkable case of predator-prey interactions with a rapidly shifting arms race dynamic. Understanding venom evolution is hence both important to our understanding of predator trait evolution as a whole and the ecology of this important predatory group.

## 4.2 INTRODUCTION

The evolution of predatory traits can often be the defining feature of whole clades of animals, from the evolution of the first jawed fish to the use of silk for web construction in arachnids. Perhaps nowhere is this better illustrated than in the evolution of venom in snakes. Through the processes of limb reduction and eventual loss beginning over 160 million years ago (Caldwell et al., 2015) snakes have relied on extreme adaptations in order to capture and kill prey items such as complex cocktails of venoms (Casewell et al., 2013; Fry et al., 2012). This reliance on venom as a primary means to capture prey in many species of snakes makes them an excellent group to study how fundamental aspects of ecology, such as habitat dimensionality, can drive the evolution of predatory traits and predator-prey interactions.

Venoms, which can be broadly defined as "a secretion produced in a specialised gland in one animal and delivered to a target animal through the infliction of a wound, which contains molecules that disrupt normal physiological or biochemical process so as to facilitate feeding or defence by the producing animal" (Casewell et al., 2013), in snakes consist of complex cocktails of proteins and other compounds creating neurotoxic and hemotoxic compounds (Greene, 1997; Casewell et al., 2013). While the biological properties these mixtures possess has lead to a wide body of biomedical research there is surprising little understanding of the

ecological pressures associated with the evolution of the diverse venoms found in snakes (Greene, 1997; Casewell et al., 2013). Functionally venoms are used for both foraging and anti-predator defence. However anti-predatory defence is likely to be secondary functionality of venoms, as reflected by the lack of correlation between lifespan and the possession of venom in snakes (Hossie et al., 2013), with aiding in prey acquisition a more likely primary function (ref). However despite the clear functionality and benefits associated with possessing venom many species of snakes have paradoxically lost this ability secondarily. Such atrophy of venom toxicity, production and of the apparatus required to deliver venom is seen at the most extreme vestigial state in the sea snake *Aipysurus eydouxii* (Li et al., 2005), but is also seen as various levels of atrophy of toxicities or venom volumes produced in other species (Fry et al., 2012). One possible solution to this paradox is the investment cost associated with the production of venoms.

Venom synthesis carries an appreciable cost both with regards to energy requirements and through possible lost opportunities. After venom extraction pitvipers have been shown to greatly increase their metabolic rates over a 72 hour periods McCue (2006), and while other species indicate less severe costs (Pintor et al., 2010), species that heavily dependent on their venom to capture prey would undergo lost opportunities over the replenishment period. This cost is reflected in the behaviours of some rattlesnake species that meter the amount of venom they inject into their prey species (HAYES, 1995) and also through the occurrence of dry bites associated with defensive behaviour (Morgenstern and King, 2013). This cost of venom explains the loss or reduction of venom in many species, for example a switch to a diet of eggs in *Aipysurus eydouxii* is likely to be the driver of venom loss in this species due to the removal of the need to incapacitate their prey. However many species of similar size and diet still show considerable variation in the toxicity and volume of venom they produce pointing towards other ecological or evolutionary drivers of venom evolution.

One key component in the evolution of venom is the identity of the target prey species. The venoms of several species of snake show a strong prey-specific element with regards to the toxicity. For example Barlow et al. (2009) showed that within *Echis* viper populations that feed on different prey groups, individuals show higher toxicities for their preferred prey items. Similarly Malaysian pit vipers show variation in their venoms that correlate with diet (Daltry et al., 1996). However such prey-specificity in venom does not seem to be present in all snakes species making the

ubiquity of this interaction unclear (Williams et al., 1988). One possible explanation for this is the arms race between the evolution of venom potency in snakes and the corresponding evolution of resistance in species under heavy predation, such as ground squirrels showing resistance to their rattlesnake predators (Poran et al., 1987). In fact there is some evidence that such resistance to pitviper venoms in Opossums has led to a switch in predator-prey roles with Opossums now the predators of pitvipers (Voss, 2013). This arms race has resulted in the rapid evolution of genes associated with venom as demonstrated in the king cobra genome (Vonk et al., 2013), however a simpler evolutionary response to such resistance may be to increase the amount of venom a species produces.

The evolution of snake toxicity depends on rapid genomic evolution, such as through gene duplication events, in order to stay apace with prey resistance (Vonk et al., 2013). Such evolutionary events are likely to be relatively rare which may result in species relying on increased venom doses in order to keep pace with short term prey resistance responses. Species which show low toxicities would hence be expected to compensate by producing larger reservoirs of venom with which to increase dosages to prey while species with high toxicities would be expected to reduce venom production in order to offset unnecessary costs (McCue, 2006). Such variation in prey resistance may also lead to "overkill" type behaviours where individuals inoculate doses far in excess of that required to incapacitate prey items (ref). This overkill behaviour is also likely to in part be an artefact to the common use of mice to determine venom toxicities instead of a snakes natural prey. A more realistic interpretation of the data requires including the physiological distance such test species may have in comparison to snakes diet. Overall a correlation between venom toxicity and volume would be expected if snakes use compensatory behaviour while species with a diet close to that of the test model would be expected to show higher toxicities indicative of adaptive prey specific venoms. While the evolution of venom is likely to be strongly influenced by the arms race between predator and prey, the ability to simply find a prey item may also be an important determinant in the volume and toxicity of a snakes venom.

While incapacitating prey is primary function of venom, venom evolution might also be expected to be influenced by the probability of encountering such a prey item. One such aspect which may influence these probabilities is habitat dimensionality (Pawar et al., 2012) as encounter rates show higher scaling with body mass in higher dimensional environments. This may decrease the investment in venom production

due to the higher probability of encountering prey reducing lost opportunities of missed strikes or though the faster replenishment rates in order to fully exploit such encounters, which may be associated with the faster digestion rates seen in arboreal species (Lillywhite et al., 2002). Conversely high habitat dimensionality may also increase the venom volume produced through the increased capacity of prey species to escape in multiple directions or selection to higher toxicities (Healy et al., 2014; Møller, 2010).

Here I use a comparative approach in order to test multiple hypothesis on venom evolution in snakes. Using data on venom toxicity, volume produced, size, diet and environment I test using a multiple response model the relationship between venom toxicity using median lethal dose as a measure and both maximum and mean venom volumes found in snakes. I also test whether species that have diets phylogenetically similar to the test animal used to determine toxicity show increased toxicities and whether species that include eggs within their diet show atrophy of both venom toxicity and volume. Finally I test whether species that inhabit high dimensional environments, namely arboreal and aquatic species, show differences in the venom volume and toxicity. Overall I find that species in high dimensional habitats or that consume eggs show a reduction in both maximum and mean venom volumes produced and also that snakes show higher toxicities to species that are physiologically closer to that found within their diet.

## 4.3 MATERIALS AND METHODS

### 4.3.1 *Data*

As a measure of venom toxicity I used median lethal dose ( $LD_{50}$ ), the individual dose required to kill 50% of a population of test animals, were lower values of  $LD_{50}$  indicate a higher venom toxicity. As the route of inoculation can affect  $LD_{50}$  (ref) only values estimated from either intravenous, subcutaneous, intrapulmonary or intramuscular inoculation routes were used, with a fixed term included to account for the variation between these routes. While most studies determine  $LD_{50}$  values using murine test animals I also included studies that used alternative models as snake venom potency is likely to be linked to diet (Barlow et al., 2009). I used both reported maximum and mean dry weight (mg) as a measure of venom volume as the dry weight represents the active proteinaceous component of venom and as it was the most available reported measure. In the case of multiple studies reported

venom volumes the mean values across the studies were taken as the value for that species with the maximum across all studies used as the overall maximum value.

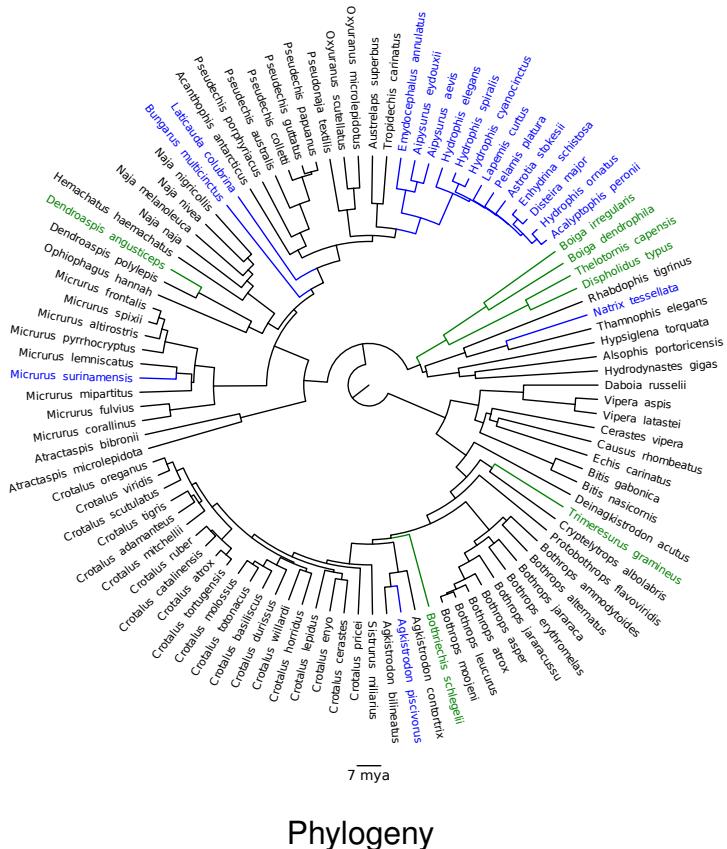
Diet data was collated from the literature using studies with quantitative estimates of prey proportions, mainly from studies of stomach contents (See appendix for data). As prey items were rarely identified to lower taxonomic levels diet was categorized as in (Allen et al., 2013) into six prey categories; invertebrates, fish, amphibians, lizards, birds and mammals. A separate term indicating the inclusion of eggs within a species diet was also included.

To test whether snakes with prey phylogenetically close to the LD<sub>50</sub> test had higher toxicities I calculated a score relating to the phylogenetic distance between the test species used to calculate the LD<sub>50</sub> value and the groups present in the snakes diet. This was calculated as the sum of the phylogenetic distance, using average estimates from TimeTree (Hedges et al., 2006), between each prey group and the LD<sub>50</sub> model by the proportion of each prey group reported in each snake species diet. For example a species with a diet of 20% mammals, 50% fish and 30% reptiles with a LD<sub>50</sub> measured using mice would have a score of 0.2(0) + 0.5(400.1) + 0.3(296) = 288.85.

Species habitat was categorised as either terrestrial, fossorial, aquatic or arboreal based on literature accounts. In order to directly test any effect of the dimensionality of habitat environment each environment was scored, as in (Pawar et al., 2012), with terrestrial and fossorial environments scored as two-dimensional and arboreal and aquatic scored as three-dimensional. As venom volume is known to increase with body size (Mirtschin et al., 2002), it was included in the analysis using total length values from the literature, primarily from the compilation of (Boback and Guyer, 2003) and from field guides and other works on regional snake faunas. To allow direct comparison with other allometric scaling studies body length was converted into mass using the conversion in (Boback and Guyer, 2003).

Mass, LD<sub>50</sub>, venom volume and phylogenetic distance between diet and model were log10 transformed, mean centred and expressed in units of standard deviation prior to analysis. Significance was determined for the fixed effects when 95% of the data is greater or less than 0. To correct for phylogeny I used the tree from (Pyron and Burbrink (2014), Figure 1).

Overall data was collated for 101 species (76 species with maximum venom volume estimates, 99 species with average venom volume estimates).

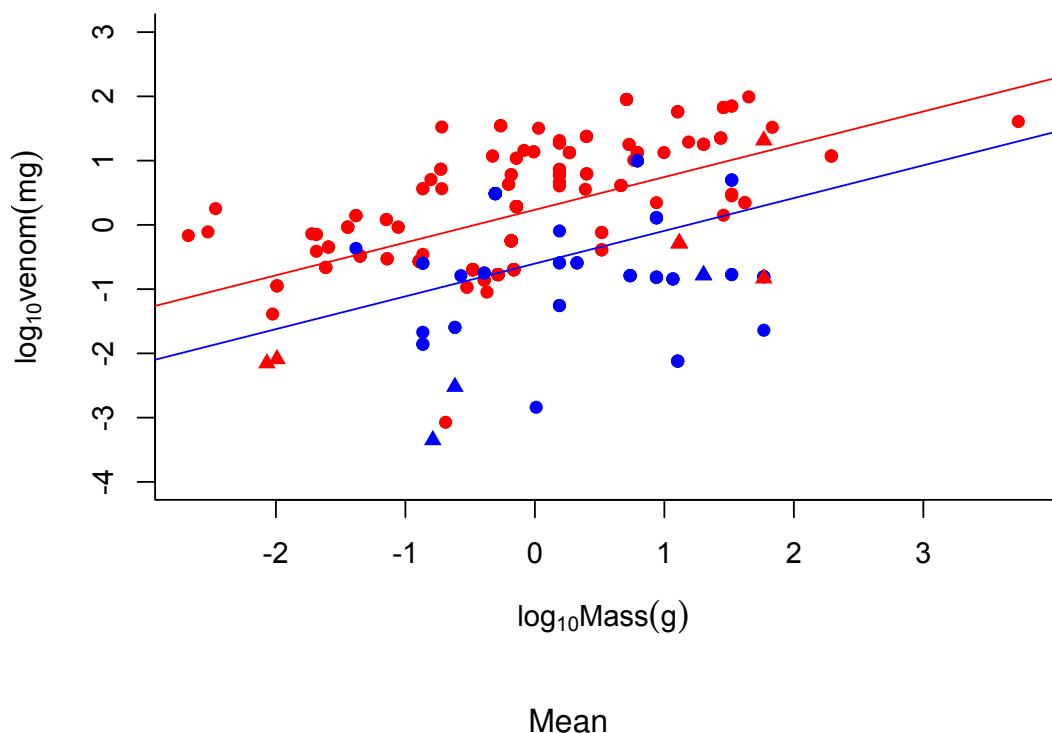


### 4.3.2 Analyses

To test these hypotheses I fit multiple response phylogenetic mixed models using the MCMCglmm package (Hadfield et al., 2010) in R 2.14.2 (R Core Team, 2014). As venom volume and LD<sub>50</sub> are likely to have co-evolved both were included as response variables with mass, LD<sub>50</sub> inoculation method, habitat dimensionality, the presence of eggs in diet and phylogenetic distance from LD<sub>50</sub> model included as explanatory variables. I fit two separate models; one using maximum venom volume and one with average venom volume. Phylogeny was controlled by including it using the animal term in the MCMCglmm model (Hadfield et al., 2010). Variation due to multiple measures on individual species, mostly to allow the inclusion of separate values for sub-species, was included using a separate random term at the species level. All models were fitted with uninformative priors by using inverse-Wishart parameter expanded priors (Hadfield et al., 2010) with burn-in, thinning and number of iterations determined to ensure effective sample sizes exceeded 1000 for all parameter estimates and convergence tested using the Gelman-Rubin statistic (Gelman and Rubin, 1992).

## 4.4 RESULTS

After controlling phylogeny these analysis showed that smaller species that inhabit high dimensional environments have both lower mean and maximum volumes of venom (Figures 1 and 2, Tables 2 and 5). Toxicity was affected by the route of inoculation, with intravenous and intrapulmonary inoculation routes showing lower LD<sub>50</sub> in comparison to subcutaneous measures, and the phylogenetic distance between the LD<sub>50</sub> model and species diet, with diets closer to the LD<sub>50</sub> model showing higher toxicities (Tables 3 and 6). Species with egg based diets showed a reduction in toxicity and maximum venom volume but not average venom volume (Tables 2,3,5,6).



There was no correlation between LD<sub>50</sub> and either maximum or mean venom volumes (Tables 1 and 4). Both LD<sub>50</sub> and venom volume show high phylogenetic variance with phylogeny showing a higher association in LD<sub>50</sub> in comparison to venom volume in both models (Tables 1 and 4).

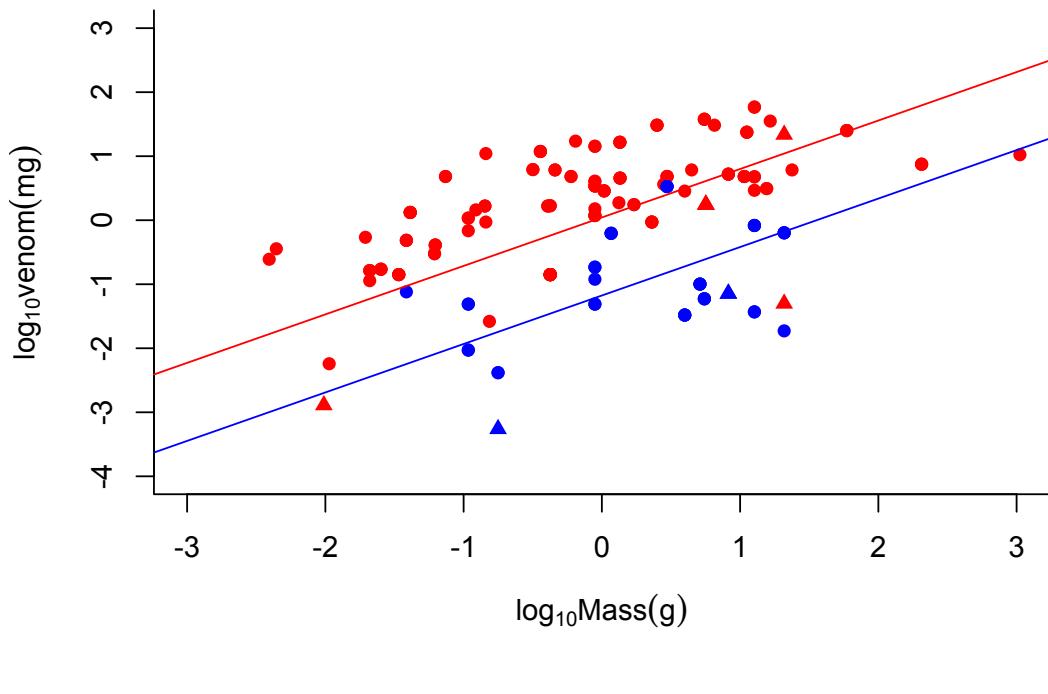


TABLE. Correlation structure on random terms.

Terms	Estimate	Lower CI	Higher CI
<b>Phylogeny</b>			
Variance: Mean volume	0.456	0.145	0.847
Covariance: Mean volume and LD <sub>50</sub>	-0.003	-0.290	0.301
Variance: LD <sub>50</sub>	0.909	0.479	1.452
<b>Residuals</b>			
Variance: Mean volume	0.009	0.007	0.011
Covariance: Mean volume and LD <sub>50</sub>	0.003	-0.004	0.011
Variance: LD <sub>50</sub>	0.268	0.215	0.328
<b>Species</b>			
Variance: Mean volume	0.308	0.156	0.462
Covariance: Mean volume and LD <sub>50</sub>	0.030	-0.040	0.118
Variance: LD <sub>50</sub>	0.055	0.001	0.170

## 4.5 DISCUSSION

These results show that, after controlling for body size and phylogeny, the evolution of venom in snakes is linked to their habitat, prey and the costs associated with producing large amounts of venom. In particular the atrophy of venom seen across venomous snakes is shown to be linked with arboreal and aquatic lifestyles, through

TABLE. Volume in average volume.

<i>Fixed Terms</i>	<i>Estimate</i>	<i>Lower CI</i>	<i>Higher CI</i>
<b>Intercept</b>	0.200	-0.161	0.567
<b>Body Mass</b>	0.510	0.442	0.564
<b>Inoculation Route</b>			
Intravenous (IV)	-0.011	-0.052	0.030
Intrapulmonary (IP)	-0.010	-0.052	0.030
Intramuscular (IM)	-0.009	-0.056	0.042
<b>Dimension 3D</b>	-0.829	-1.286	-0.396
<b>Eggs in diet</b>	-0.741	-1.325	-0.206
<b>Phylogenetic disparity of diet to model</b>	-0.003	-0.029	0.019

TABLE. Id50 in average volume model

<i>Fixed Terms</i>	<i>Estimate</i>	<i>Lower CI</i>	<i>Higher CI</i>
<b>Intercept</b>	0.200	-0.161	0.567
<b>Body Mass</b>	0.134	0.016	0.262
<b>Inoculation Route</b>			
Intravenous (IV)	-0.624	-0.842	-0.435
Intrapulmonary (IP)	-0.537	-0.746	-0.309
Intramuscular (IM)	-0.228	-0.455	0.049
<b>Dimension 3D</b>	-0.202	-0.670	0.243
<b>Eggs in diet</b>	0.457	-0.187	1.065
<b>Phylogenetic disparity of diet to model</b>	0.360	0.248	0.463

TABLE. Correlation structure on random terms in maximum venom

<i>Terms</i>	<i>Estimate</i>	<i>Lower CI</i>	<i>Higher CI</i>
<b>Phylogeny</b>			
Variance: Maximum volume	0.500	0.156	0.960
Covariance: Maximum volume and LD <sub>50</sub>	0.156	-0.181	0.496
Variance: LD <sub>50</sub>	0.901	0.349	1.477
<b>Residuals</b>			
Variance: Maximum volume	0.003	0.002	0.004
Covariance: Maximum volume and LD <sub>50</sub>	0.006	0.001	0.012
Variance: LD <sub>50</sub>	0.275	0.001	0.361
<b>Species</b>			
Variance: Maximum volume	0.230	0.103	0.373
Covariance: Maximum volume and LD <sub>50</sub>	-0.036	-0.141	0.052
Variance: LD <sub>50</sub>	0.061	0.001	0.188

a reduction of venom volumes, and, in the case of maximum venom volume, transitions to a diet of eggs. This is likely due to the costs of producing venom (Pintor

TABLE. Volume in Maximum volume.

<i>Fixed Terms</i>	<i>Estimate</i>	<i>Lower CI</i>	<i>Higher CI</i>
<b>Intercept</b>	0.043	-0.339	0.379
<b>Body Mass</b>	0.757	0.708	0.797
<b>Inoculation Route</b>			
Intravenous (IV)	-0.006	-0.031	0.019
Intrapulmonary (IP)	0.008	-0.019	0.037
Intramuscular (IM)	0.003	-0.037	0.047
<b>Dimension 3D</b>	-1.212	-1.638	-0.763
<b>Eggs in diet</b>	-0.564	-1.219	0.063
<b>Phylogenetic disparity of diet to model</b>	-0.001	-0.032	0.033

TABLE. Id50 in maximum volume model

<i>Fixed Terms</i>	<i>Estimate</i>	<i>Lower CI</i>	<i>Higher CI</i>
<b>Intercept</b>	0.043	-0.339	0.379
<b>Body Mass</b>	0.145	-0.018	0.305
<b>Inoculation Route</b>			
Intravenous (IV)	-0.656	-0.892	-0.440
Intrapulmonary (IP)	-0.561	-0.804	-0.326
Intramuscular (IM)	-0.191	-0.531	0.152
<b>Dimension 3D</b>	0.240	-0.300	0.836
<b>Eggs in diet</b>	0.705	0.076	1.510
<b>Phylogenetic disparity of diet to model</b>	0.251	0.080	0.436

et al., 2010) outweighing the benefits of producing and maintaining large amount of venom in species in higher dimensions.

One of the drivers behind such as reduced benefit of venom production for species in three dimensional environments may be the expected increased probability of encountering prey items in such environments (Pawar et al., 2012). This would result in species being under less selection pressures to maintain the larger reservoirs of venom required to respond to the rarer event of encountering a prey item in low dimensional environment. The biomechanical limitations of arboreal lifestyles is also suggested to leading to faster digestion rates in these species (Lillywhite et al., 2002), which in turn may lead to smaller venom volumes which would facilitate faster venom replenishment rates. The limitations affecting predators in these environments would also restricts prey body size in arboreal species. Likewise marine snakes are also known to feed disproportionately on smaller fish than expected (Voris and Moffett, 1981). Since some species are known to meter

venom depending on prey size (HAYES, 1995), it may be the size distribution of prey available in these habitats that influences the evolution of venom volume. Hence although the patterns of venom volumes are clearly related to a snakes habitat a snakes prey may be still be the main driver of these differences.

While the pattern of associating within these habitats is clear another explanation to this association between small venom volumes and high dimensionality is that prey items in such environments are smaller. Arboreal environment are extremely selective with regards to size meaning such snakes species are likely to encounter smaller prey items more often then expected then in terrestrial environments. Aquatic snakes are also known for selecting smaller prey items. Data on prey size is hence likely to further the understanding of venom evolution along with the insights of the importance of prey identity.

The nature of a snakes diet was also found to affect venom toxicity and to a lesser extent venom volume. Species with even small proportions of eggs in their diets show both reduced maximum venom volumes and lower venom toxicities. This is unsurprising as the benefits of venom to an oviparous diet are likely to be low (Li et al., 2005). This atrophy in oviparous snakes also reaffirms the primary foraging function of venom with any digestive (Rodríguez-Robles and Thomas, 1992) or defensive functions (Jansa and Voss, 2011) being secondary benefits. However these results should be interpreted with caution due to the low number oviparous species within the analysis (eight with only four having greater than 20% in their diet) with further data required to fully gauge the evolutionary role of egg eating in snakes. Apart from the reduction of the venom apparatus in species which show a shift from carnivory to oviparity (Li et al., 2005), these results also show that snake venom toxicity is prey-specific. While prey specificity has been shown within particular groups of snakes (Barlow et al., 2009,?; Richards et al., 2012) this is the first study to show venom prey specificity across all venomous snakes. This result of increased toxicity with reduced phylogenetic distance between diet LD<sub>50</sub> model suggests that while there are several cases of prey species developing resistance to venom (Lillywhite et al., 2002), snakes in general are "ahead" in the arms race between prey venom resistance and predator venom toxicity.

While these results further demonstrate the arms race venom evolution is locked within they also surprisingly show no evidence of co-evolution between venom volume and venom toxicity evolution. It would be expected that species with low toxicities may evolve compensatory mechanisms such as increased venom volumes

to allow them to overcome prey resistance. While the historical lack of appropriate model species for calculating LD<sub>50</sub> may account for the underestimation of toxicity levels in some species, even after accounting for such species mismatching here there is no evidence of a correlation between these two aspects of venom functionality. This lack of compensatory evolution may instead be explained by changes in behaviour with species with low toxicities combining the use of venom along with prey holding or constriction in order to incapacitate prey Shine and Schwaner (1985).

While volume and LD<sub>50</sub> show no co-variance both traits do show strong phylogenetic effects suggesting evolutionary constraints also partially explain the variation in venom lethality and volume across snakes. As expected, LD<sub>50</sub> evolution shows a higher constraint in comparison to venom volume evolution. This is likely to be a reflection of the requirement for major genetic changes, such as gene duplication events, in order to increase venom toxicity (Vonk et al., 2013). While venom volume shows less phylogenetic autocorrelation the physiological requirements necessary to house large volumes of venom is likely to be the main limitation in many rear fanged groups. However many rear fanged snakes such as species of mamba can contain venom volumes similar to that of many front fanged species.

Overall this study shows that across venomous snakes ecological factors associated with predator-prey interactions drive the evolution of venom. While further studies are required to understand the complex nature of predatory trait evolution these results show that fundamental aspects of predator-prey interactions including size, habitat dimensionality and evolutionary constraints can help understand one of the most medically important and iconic predatory traits, venom.

## CHAPTER 5

## DISCUSSION

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### 5.1 CONSIDERING DIMENSIONS

One of the central goals in ecology and evolution is to understand the complexity of the biological world. There has been several approaches towards simplifying this complexity including the top down approaches of the metabolic theory of ecology (Brown et al., 2004), the bottom up approach of dynamic energy budget theory (Kooijman, 2009) and the entropy based approach of MaxEnt (Harte et al., 2008). However whatever the approach certain elements of our world must be included in such macroevolutionary approaches in order for such models to accurately reflect the reality of nature.

Here I have attempted here to make the case for the importance of including perhaps one of the most fundamental elements of physical reality, its dimensions. While all life is embedded within the three spatial and one temporal dimension of the universe, how species exploit or interact within these dimensions can determine the nature of many biological interactions. This is reflected in the results of the above analysis which demonstrate the important influence of the ability of a species to exploit these dimensions affecting how they see the world, how long they live in it and how they make a living.

While this thesis focuses on how traits associated with predator-prey interactions (spotting, escaping or capturing) are affected by environment dimensionality, these effects are likely to hold important consequences for larger ecological systems in particular through the strong influence of predator-prey interacts. For example trophic interaction strengths have important influences on ecosystem stability leading to the persistence of certain types of systems. Likewise by including the dimensions over which species interact can help understand the diversity of physiologies found in nature. For example the new endothermic fish.

While these factors are likely to be important across biological systems many of the questions outlined within this thesis were restricted by limitations in data

availability. While large data sources of data related to MET, such as metabolic rates and body sizes, are now available other data relating to fundamental aspects of ecology are still in the early stages accumulation. For example data on species behaviour, diets, sensory capabilities and other morphological traits can be still surprisingly sparse, and when available relatively coarse in their nature. These data however, as demonstrated above, can still provide starting points to test many predicted patterns in nature through comparative analysis. Even with the increase body of data continuously growing and becoming more readily available, such as xxxx, future directions including comparative methods on new datasets or separate approaches are likely to offer the best prospects.

## 5.2 FUTURE DIRECTIONS

### 5.2.1 *Comparative methods*

Throughout this thesis the comparative method employed grew to match the increasing complexity of the hypotheses explored throughout my PhD. From standard PGLS models in Chapter one, to the inclusion of the error associated with phylogeny construction in Chapter 2, to the multiple response models used in the final chapter the increased complexity of these models were important to test the questions posed in these chapters. These methods will continue to be useful with regards to questions posed in each of the chapters presented here.

Since publication of my work on temporal perception (Healy et al., 2013) numerous studies on the sensory perceptual abilities of species in particular ecological settings, such as deep sea foraging species fish (Kalinowski et al., 2014; Wegner et al., 2015; Landgren et al., 2014), or on the effects such sensory limitations can incur on their behaviour and ecology (Bar et al., 2015; Inger et al., 2014). These studies represent the growing interest within this field and the additional data on temporal perception that may allow for more nuanced analysis between species ecologies and their temporal perceptual abilities. Other interesting avenues to explore would be other sensory systems, including olfactory, auditory and tactile. Echolocation is likely to be a particularly fruitful sense to study sensory limitations on predator-prey interactions, in particular through comparison of body size ranges from the smallest mammals (bats and shrews) to the largest predators (sperm whales).

The second chapter of this thesis took advantage of the Bayesian nature of the MCMCglmm comparative approach of (Hadfield et al., 2010) in order to include the

error associated with constructing a phylogeny. This is likely to prove useful in future approaches as Bayesian generated phylogenies become more available and within groups were phylogeny topology is still debated. In fact the difference of using this approach was shown with regards to the methods used by Williams and Shattuck (2015) in response to Healy et al. (2014) showing that both eusociality and fossoriality are important to lifespan evolution, whereas the approach used in chapter 2 differed in showing that eusociality but not fossoriality was important. Irrespective of methodology, these result brings into question the importance of fossoriality in the evolution of longevity, however recently other lines of evidence conflict on its importance (Faulkes et al., 2015). Large comparative analysis between fossorial and non-fossorial species in groups such as amphibians and reptiles may help to resolve this conflict. Another useful future direction on comparative analysis in lifespan evolution is to test whether species that can avail of high dimensional escape routes show differences in life-history traits. In particular pelagic and benthic marine species are likely to provide a good test case for this hypothesis.

The final chapter is yet to be published however the need for further comparative analysis is clear following the results provided above. In particular the inclusion of prey body size data is likely to be important with regards to the affect of habitat dimensionality on snake venom volumes. Following the association between species that are ovivorous or in high dimensional habitats and the atrophy of venom seen in the results of chapter 4, a larger analysis comparing ecology of venomous and completely non venomous species.

In particular an analysis of the complete absence of venom apparatus within snakes may yield further insights to the apparent atrophy seen in this chapter. As a complete phylogeny of snakes has only recently appeared the opportunity to do this across the whole group has only become achievable.

### 5.2.2 *Other approaches*

While comparative methods feature as the central method in this thesis such approaches are generally limited in their scope to identifying large scale macro ecological and evolutionary patterns. For example due to the lack of appropriate data on sensory ability the ecological drivers of temporal ability is outside of the range of such approaches. Likewise the dimensionality of escape space open to a species is often heavily correlated with other aspects of ecological and life-history traits make

decoupling such causalities difficult. One such approach which would be particularly beneficial for this question is to link together agent based modelling with neural network modelling.

Agent based modelling uses simulations of individual "agents" that are defined by simple sets of rules. Unlike experimental approaches agent based modelling allows the full set of parameter space to be explored making this an ideal approach for questions featuring fundamental constraints such as dimensionality. In the case of temporal perception evolution such rules are relatively simple; predict the future position of a moving target using displaying different movement patterns. However while this approach may encapsulate the absolute limits at which temporal perception no longer improves target predictions the neural and metabolic costs associated with such perceptual abilities, as demonstrated in chapter 2, need to be incorporated. Neural networks would provide one such solution however allowing for a more evolutionary approach to optimal temporal perception while also allowing for the ability to test a series of other related questions including the optimal temporal perceptions for a series of different prey motion patterns. The neural network approach would also be able to be extended outside of the simulated environment provided by the agent based modelling through the use of robots. Robots are essentially an agent based model parametrise within reality, making them an ideal half-way house between simulations and experimental approaches (Floreano and Keller, 2010). Furthermore, while being used to study predator-prey interactions they inadvertently displayed behaviours associated with limitations of their temporal perceptual abilities. In particular due to the refresh rates of the cameras used for target tracking and navigation the robots were found to only move at intermediate speeds despite being capable of much higher speeds.

Such use of simulated environments may also be applicable to further investigations on the importance of the dimensionality of a species escape space. By extending the agent based modelling approach towards incorporating the geometric predator escape models of Howland (1974) the importance of dimensionality can be tested directly within a range of contexts. For example the importance of this escape space could be used to study fish escape strategies (Domenici and Blake, 1997) and even extending into the importance of shaoling behaviour in response to shark and whale predations by incorporating the simple behaviour rules of (Couzin et al., 2002).

These approaches could also be extended outside of the simulated environment provided by the agent based models through the use of robots. Robots are essentially an agent based model parametrise within reality, making them an ideal half-way house between simulations and experimental approaches (Florenzano and Keller, 2010). Furthermore, while being used to study predator-prey interactions they inadvertently displayed behaviours associated with limitations of their temporal perceptual abilities. In particular due to the refresh rates of the cameras used for target tracking and navigation the robots were found to only move at intermediate speeds despite being capable of much higher speeds. The use of robots to incorporate realistic parameters into such model is also not constraint to terrestrial systems with the aerial robofly (Lauder, 2001) and aquatic robofish (Faria et al., 2010).

Whatever the approach, future research into how biology fits into and exploits the fundamental aspects of our reality is likely to continue along its current fruitful trajectory. As the most complex entity in the universe it should be no surprise that many of the elements and behaviours of biological systems are still so difficult to predict or understand. By comparing biology to other complex systems both mathematical and real we should be able to further delve into the most mysterious element of existence.

## BIBLIOGRAPHY

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- Albert EM, San Mauro D, García-París M, Rüber L, Zardoya R (2009) Effect of taxon sampling on recovering the phylogeny of squamate reptiles based on complete mitochondrial genome and nuclear gene sequence data. *Gene* 441: 12–21.
- Ali MA, Klyne MA (1985) Vision in vertebrates. Plenum Press New York.
- Allen WL, Baddeley R, Scott-Samuel NE, Cuthill IC (2013) The evolution and function of pattern diversity in snakes. *Behavioral Ecology* 24: 1237–1250.
- Alroy J, Aberhan M, Bottjer DJ, Foote M, Fürsich FT, et al. (2008) Phanerozoic trends in the global diversity of marine invertebrates. *Science* 321: 97–100.
- Austad SN, Fischer KE (1991) Mammalian aging, metabolism, and ecology: evidence from the bats and marsupials. *Journal of Gerontology* 46: B47–B53.
- Autrum H (1958) Electrophysiological analysis of the visual systems in insects. *Experimental cell research* 14: 426.
- Bahill T, Baldwin DG (2004) The rising fastball and other perceptual illusions of batters. In: Biomedical Engineering Principles in Sports, pp. 257–287, Springer.
- Bar NS, Skogestad S, Marçal JM, Ulanovsky N, Yovel Y (2015) A Sensory-Motor Control Model of Animal Flight Explains Why Bats Fly Differently in Light Versus Dark. *PLoS biology* 13: e1002046–e1002046.
- Barlow A, Pook CE, Harrison RA, Wüster W (2009) Coevolution of diet and prey-specific venom activity supports the role of selection in snake venom evolution. *Proceedings of the Royal Society B: Biological Sciences* 276: 2443–2449.
- Benton MJ, Donoghue PC (2007) Paleontological evidence to date the tree of life. *Molecular biology and evolution* 24: 26–53.
- Biewener AA (2003) Animal locomotion. Oxford University Press.
- Bininda-Emonds OR, Cardillo M, Jones KE, MacPhee RD, Beck RM, et al. (2007) The delayed rise of present-day mammals. *Nature* 446: 507–512.
- Block BA, Carey FG (1985) Warm brain and eye temperatures in sharks. *Journal of Comparative Physiology B* 156: 229–236.

- Boback SM, Guyer C (2003) Empirical evidence for an optimal body size in snakes. *Evolution* 57: 345–451.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) TOWARD A METABOLIC THEORY OF ECOLOGY. *Ecology* 85: 1771–1789, URL <http://dx.doi.org/10.1890/03-9000>.
- Brown JW, Rest JS, García-Moreno J, Sorenson MD, Mindell DP (2008) Strong mitochondrial DNA support for a Cretaceous origin of modern avian lineages. *BMC biology* 6: 6.
- Buffenstein R, Jarvis JU (2002) The naked mole rat—a new record for the oldest living rodent. *Science's SAGE KE* 2002: 7.
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.
- Caldwell MW, Nydam RL, Palci A, Pesteguía S (2015) The oldest known snakes from the Middle Jurassic-Lower Cretaceous provide insights on snake evolution. *Nature communications* 6.
- Carey FG (1982) A brain heater in the swordfish. *Science* 216: 1327–1329.
- Carwardine M (1995) The Guinness book of animal records. Guinness Publishing.
- Casewell NR, Wüster W, Vonk FJ, Harrison RA, Fry BG (2013) Complex cocktails: the evolutionary novelty of venoms. *Trends in ecology & evolution* 28: 219–229.
- Chatterjee S, Templin RJ, Campbell KE (2007) The aerodynamics of Argentavis, the world's largest flying bird from the Miocene of Argentina. *Proceedings of the National Academy of Sciences* 104: 12398–12403.
- Clark RW, Tangco S, Barbour MA (2012) Field video recordings reveal factors influencing predatory strike success of free-ranging rattlesnakes (*Crotalus* spp.). *Animal Behaviour* 84: 183–190.
- Cohen JE, Briand F, Newman CM (1990) Community food webs: data and theory.
- Couzin I, Krause J, James R, Ruxton G, Franks N (2002) The collective behaviour of animal groups in three dimensional space. *Journal of Theoretical Biology* 218: 1–11.
- Cramp S (1977) Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the western Palearctic. Vol. 1, Ostrich to ducks. Oxford University Press.

- Crognale MA, Eckert SA, Levenson DH, Harms CA (2008) Leatherback sea turtle *Dermochelys coriacea* visual capacities and potential reduction of bycatch by pelagic longline fisheries. *Endangered Species Research* 5: 249–256.
- Cronin T (2005) The role of vision in predatore prey interactions. *Ecology of Predator* p. 1.
- Daltry JC, Wüster W, Thorpe RS (1996) Diet and snake venom evolution. *Nature* 379: 537–540.
- De Magalhaes J, Costa J (2009) A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology* 22: 1770–1774.
- De Magalhães JP, Costa J, Church GM (2007) An analysis of the relationship between metabolism, developmental schedules, and longevity using phylogenetic independent contrasts. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences* 62: 149–160.
- D'EATH RB (1998) Can video images imitate real stimuli in animal behaviour experiments? *Biological Reviews* 73: 267–292.
- Depczynski M, Bellwood DR (2005) Shortest recorded vertebrate lifespan found in a coral reef fish. *Current Biology* 15: R288–R289.
- Dessing JC, Craig CM (2010) Bending it like Beckham: how to visually fool the goalkeeper. *PLoS One* 5: e13161.
- Domenici P, Blake R (1997) The kinematics and performance of fish fast-start swimming. *Journal of Experimental Biology* 200: 1165–1178.
- Dudley R (2002) Mechanisms and implications of animal flight maneuverability. *Integrative and Comparative Biology* 42: 135–140.
- Faria JJ, Dyer JR, Clément RO, Couzin ID, Holt N, et al. (2010) A novel method for investigating the collective behaviour of fish: introducing âĂĲRobofishâĂŹ. *Behavioral Ecology and Sociobiology* 64: 1211–1218.
- Faulkes CG, Davies KT, Rossiter SJ, Bennett NC (2015) Molecular evolution of the hyaluronan synthase 2 gene in mammals: implications for adaptations to the subterranean niche and cancer resistance. *Biology letters* 11: 20150185.
- Ferry ES (1892) Persistence of vision. *American Journal of Science* pp. 192–207.
- Floreano D, Keller L (2010) Evolution of adaptive behaviour in robots by means of Darwinian selection. *PLoS biology* 8: e1000292.

- Folkow LP, Nordøy ES, Blix AS (2004) Distribution and diving behaviour of harp seals (*Pagophilus groenlandicus*) from the Greenland Sea stock. *Polar Biology* 27: 281–298.
- Frank TM (1999) Comparative study of temporal resolution in the visual systems of mesopelagic crustaceans. *The Biological Bulletin* 196: 137–144.
- Frank TM, Johnsen S, Cronin TW (2012) Light and vision in the deep-sea benthos: II. Vision in deep-sea crustaceans. *The Journal of experimental biology* 215: 3344–3353.
- Franz A, Ronacher B (2002) Temperature dependence of temporal resolution in an insect nervous system. *Journal of Comparative Physiology A* 188: 261–271.
- Freckleton R (2009) The seven deadly sins of comparative analysis. *Journal of evolutionary biology* 22: 1367–1375.
- Fritsches KA, Brill RW, Warrant EJ (2005) Warm eyes provide superior vision in swordfishes. *Current Biology* 15: 55–58.
- Froese R, Pauly D (2012) FishBase ([www.fishbase.org](http://www.fishbase.org)). World wide web electronic publication .
- Fry BG, Casewell NR, Wüster W, Vidal N, Young B, et al. (2012) The structural and functional diversification of the Toxicofera reptile venom system. *Toxicon* 60: 434–448.
- Fry CH, Fry K (2010) Kingfishers, bee-eaters and rollers. A&C Black.
- Garamszegi LZ, Møller AP, Erritzøe J (2002) Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proceedings of the Royal Society of London B: Biological Sciences* 269: 961–967.
- Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. *Statistical science* pp. 457–472.
- Gilbert C (1997) Visual control of cursorial prey pursuit by tiger beetles (Cicindelidae). *Journal of Comparative Physiology A* 181: 217–230.
- Greene HW (1997) Snakes: the evolution of mystery in nature. Univ of California Press.
- Haddock SH, Dunn CW, Pugh PR, Schnitzler CE (2005) Bioluminescent and red-fluorescent lures in a deep-sea siphonophore. *Science* 309: 263–263.

- Hadfield JD, et al. (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* 33: 1–22.
- Hagura N, Kanai R, Orgs G, Haggard P (2012) Ready steady slow: action preparation slows the subjective passage of time. *Proceedings of the Royal Society B: Biological Sciences* p. rspb20121339.
- Harte J, Zillio T, Conlisk E, Smith A (2008) Maximum entropy and the state-variable approach to macroecology. *Ecology* 89: 2700–2711.
- Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology, vol. 239. Oxford university press Oxford.
- HAYES WK (1995) Venom metering by juvenile prairie rattlesnakes, *Crotalus v. viridis*: effects of prey size and experience. *Animal Behaviour* 50: 33–40.
- Healy K, Guillerme T, Finlay S, Kane A, Kelly SB, et al. (2014) Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proceedings of the Royal Society B: Biological Sciences* 281: 20140298.
- Healy K, McNally L, Ruxton GD, Cooper N, Jackson AL (2013) Metabolic rate and body size are linked with perception of temporal information. *Animal behaviour* 86: 685–696.
- Hedges SB, Dudley J, Kumar S (2006) TimeTree: a public knowledge-base of divergence times among organisms. *Bioinformatics* 22: 2971–2972.
- Hedrick TL (2011) Damping in flapping flight and its implications for manoeuvring, scaling and evolution. *The Journal of experimental biology* 214: 4073–4081.
- Heglund NC, Taylor CR (1988) Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *Journal of Experimental Biology* 138: 301–318.
- Heim NA, Knope ML, Schaal EK, Wang SC, Payne JL (2015) CopeâŽs rule in the evolution of marine animals. *Science* 347: 867–870.
- Holmes D, Ottinger M (2003) Birds as long-lived animal models for the study of aging. *Experimental gerontology* 38: 1365–1375.
- Holmes DJ, Austad SN (1994) Fly now, die later: life-history correlates of gliding and flying in mammals. *Journal of Mammalogy* pp. 224–226.

- Hornstein E, O'Carroll D, Anderson J, Laughlin S (2000) Sexual dimorphism matches photoreceptor performance to behavioural requirements. *Proceedings of the Royal Society of London Series B: Biological Sciences* 267: 2111–2117.
- Hossie TJ, Hassall C, Knee W, Sherratt TN (2013) Species with a chemical defence, but not chemical offence, live longer. *Journal of evolutionary biology* 26: 1598–1602.
- Howland HC (1974) Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *Journal of theoretical Biology* 47: 333–350.
- Howland HC, Merola S, Basarab JR (2004) The allometry and scaling of the size of vertebrate eyes. *Vision research* 44: 2043–2065.
- Hoyo Jd, Elliott A, Sargatal J (1992) *Handbook of the Birds of the World*: Vol 1: Ostrich to Ducks. Lynx.
- Hulbert A, Pamplona R, Buffenstein R, Buttemer W (2007) Life and death: metabolic rate, membrane composition, and life span of animals. *Physiological Reviews* 87: 1175–1213.
- Inger R, Bennie J, Davies TW, Gaston KJ (2014) Potential biological and ecological effects of flickering artificial light. *PloS one* 9: e98631.
- Jánossy D (2011) *Pleistocene vertebrate faunas of Hungary*. Elsevier.
- Jansa SA, Voss RS (2011) Adaptive evolution of the venom-targeted vWF protein in opossums that eat pitvipers. *PLoS One* 6: e20997.
- Jetz W, Thomas G, Joy J, Hartmann K, Mooers A (2012) The global diversity of birds in space and time. *Nature* 491: 444–448.
- Jones G, Rydell J (1994) Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society B: Biological Sciences* 346: 445–455.
- Jordan LK, Mandelman JW, McComb DM, Fordham SV, Carlson JK, et al. (2013) Linking sensory biology and fisheries bycatch reduction in elasmobranch fishes: a review with new directions for research. *Conservation Physiology* 1: cot002.

- Kalinowski M, Hirons A, Horodysky A, Brill R (2014) Spectral sensitivity, luminous sensitivity, and temporal resolution of the visual systems in three sympatric temperate coastal shark species. *Journal of Comparative Physiology A* 200: 997–1013.
- Keller L, Genoud M (1997) Extraordinary lifespans in ants: a test of evolutionary theories of ageing. *Nature* 389: 958–960.
- Kleiber M (1947) Body size and metabolic rate. *Physiol rev* 27: 511–541.
- Kooijman SALM (2009) Dynamic energy budget theory for metabolic organisation. Cambridge university press.
- Kreysing M, Pusch R, Haverkate D, Landsberger M, Engelmann J, et al. (2012) Photonic crystal light collectors in fish retina improve vision in turbid water. *Science* 336: 1700–1703.
- Kuhn TS, Mooers AØ, Thomas GH (2011) A simple polytomy resolver for dated phylogenies. *Methods in Ecology and Evolution* 2: 427–436.
- Land MF, Collett T (1974) Chasing behaviour of houseflies (*Fannia canicularis*). *Journal of comparative physiology* 89: 331–357.
- Landgren E, Fritsches K, Brill R, Warrant E (2014) The visual ecology of a deep-sea fish, the escolar *Lepidocybium flavobrunneum* (Smith, 1843). *Philosophical Transactions of the Royal Society B: Biological Sciences* 369: 20130039.
- Lauder GV (2001) Aerodynamics: Flight of the robofly. *Nature* 412: 688–689.
- Laughlin S, Weckström M (1993) Fast and slow photoreceptors—A comparative study of the functional diversity of coding and conductances in the Diptera. *Journal of Comparative Physiology A* 172: 593–609.
- Laughlin SB (2001) Energy as a constraint on the coding and processing of sensory information. *Current opinion in neurobiology* 11: 475–480.
- Li C, Lu G, Orti G (2008) Optimal data partitioning and a test case for ray-finned fishes (Actinopterygii) based on ten nuclear loci. *Systematic Biology* 57: 519–539.
- Li M, Fry B, Kini RM (2005) Eggs-only diet: its implications for the toxin profile changes and ecology of the marbled sea snake (*Aipysurus eydouxii*). *Journal of Molecular Evolution* 60: 81–89.

- Lillywhite HB, de Delva P, Noonan BP, Schuett G, Höggren M, et al. (2002) Patterns of gut passage time and the chronic retention of fecal mass in viperid snakes. *Biology of the vipers* pp. 497–506.
- Lim DD, Motta P, Mara K, Martin AP (2010) Phylogeny of hammerhead sharks (Family Sphyrnidae) inferred from mitochondrial and nuclear genes. *Molecular phylogenetics and evolution* 55: 572–579.
- Lindstedt S, Calder III W (1981) Body size, physiological time, and longevity of homeothermic animals. *Quarterly Review of Biology* pp. 1–16.
- Lisney TJ, Rubene D, Rózsa J, Løvlie H, Håstad O, et al. (2011) Behavioural assessment of flicker fusion frequency in chicken *Gallus gallus domesticus*. *Vision research* 51: 1324–1332.
- Little A, Lougheed S, Moyes C (2010) Evolutionary affinity of billfishes (Xiphiidae and Istiophoridae) and flatfishes (Pleuronectiformes): Independent and trans-subordinal origins of endothermy in teleost fishes. *Molecular Phylogenetics and Evolution* 56: 897–904.
- Makarieva AM, Gorshkov VG, Li BL, Chown SL, Reich PB, et al. (2008) Mean mass-specific metabolic rates are strikingly similar across life's major domains: evidence for life's metabolic optimum. *Proceedings of the National Academy of Sciences* 105: 16994–16999.
- McCue MD (2006) Cost of producing venom in three North American pitviper species. *Journal Information* 2006.
- Mercer JM, Roth VL (2003) The effects of Cenozoic global change on squirrel phylogeny. *Science* 299: 1568–1572.
- Mirtschin P, Shine R, Nias T, Dunstan N, Hough B, et al. (2002) Influences on venom yield in Australian tigersnakes (*Notechis scutatus*) and brownsnakes (*Pseudonaja textilis*: Elapidae, Serpentes). *Toxicon* 40: 1581–1592.
- Møller A (2010) Up, up, and away: relative importance of horizontal and vertical escape from predators for survival and senescence. *Journal of evolutionary biology* 23: 1689–1698.
- Moorad JA, Promislow DE (2010) Evolution: aging up a tree? *Current Biology* 20: R406–R408.
- Morgenstern D, King GF (2013) The venom optimization hypothesis revisited. *Toxicon* 63: 120–128.

- Morse D, Lawton J, Dodson M, Williamson M, et al. (1985) Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* 314: 731–733.
- Murphy WJ, Pringle TH, Crider TA, Springer MS, Miller W (2007) Using genomic data to unravel the root of the placental mammal phylogeny. *Genome Research* 17: 413–421.
- Myers P, Espinosa R, Parr C, Jones T, Hammond G, et al. (2006) The animal diversity web. Accessed October 12: 2.
- Naro-Maciel E, Le M, FitzSimmons NN, Amato G (2008) Evolutionary relationships of marine turtles: a molecular phylogeny based on nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution* 49: 659–662.
- Nowak RM (1999) Walker's mammals of the world, vol. 1. JHU Press.
- Orme C, Freckleton R, Thomas G, Petzoldt T, Fritz S, et al. (2011) CAPER: comparative analysis of phylogenetics and evolution in R, R package v. 0.4. See: <http://CRAN.R-project.org/package=caper> (accessed 25 October 2011) .
- Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.
- Palmer JM, Grant BG (2010) The art of radiometry. SPIE Press Bellingham.
- Parham JF, Donoghue PC, Bell CJ, Calway TD, Head JJ, et al. (2011) Best practices for justifying fossil calibrations. *Systematic Biology* p. syr107.
- Parr M, Juniper T (2010) Parrots: a guide to parrots of the world. Bloomsbury Publishing.
- Partridge L, Barton NH (1993) Optimality, mutation and the evolution of ageing. *NATURE-LONDON-* 362: 305–305.
- Pawar S, Dell AI, Savage VM (2012) Dimensionality of consumer search space drives trophic interaction strengths. *Nature* 486: 485–489.
- Perelman P, Johnson WE, Roos C, Seuánez HN, Horvath JE, et al. (2011) A molecular phylogeny of living primates. *PLoS genetics* 7: e1001342.
- Pimm SL (1984) The complexity and stability of ecosystems. *Nature* 307: 321–326.
- Pintor AF, Krockenberger AK, Seymour JE (2010) Costs of venom production in the common death adder (*Acanthophis antarcticus*). *Toxicon* 56: 1035–1042.
- Plummer M, Best N, Cowles K, Vines K (2006) CODA: Convergence diagnosis and output analysis for MCMC. *R news* 6: 7–11.

- Pomeroy D (1990) Why fly? The possible benefits for lower mortality. *Biological Journal of the Linnean Society* 40: 53–65.
- Poran NS, Coss RG, Benjamini E (1987) Resistance of California ground squirrels (*Spermophilus beecheyi*) to the venom of the northern Pacific rattlesnake (*Crotalus viridis oreganus*): a study of adaptive variation. *Toxicon* 25: 767–777.
- Porter TC (1902) Contributions to the study of flicker. Paper II. *Proceedings of the Royal Society of London* 70: 313–329.
- Promislow DE (1993) On size and survival: progress and pitfalls in the allometry of life span. *Journal of gerontology* 48: B115–B123.
- Promislow DE, Harvey PH (1990) Living fast and dying young: A comparative analysis of life-history variation among mammals. *Journal of Zoology* 220: 417–437.
- Prugh LR, Golden CD (2014) Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of animal ecology* 83: 504–514.
- Pyron RA, Burbrink FT (2014) Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecology letters* 17: 13–21.
- R Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL <http://www.R-project.org>.
- Reisz RR, Müller J (2004) Molecular timescales and the fossil record: a paleontological perspective. *TRENDS in Genetics* 20: 237–241.
- Richards D, Barlow A, Wüster W (2012) Venom lethality and diet: Differential responses of natural prey and model organisms to the venom of the saw-scaled vipers (*Echis*). *Toxicon* 59: 110–116.
- Ricklefs RE (2010a) Insights from comparative analyses of aging in birds and mammals. *Aging cell* 9: 273–284.
- Ricklefs RE (2010b) Life-history connections to rates of aging in terrestrial vertebrates. *Proceedings of the National Academy of Sciences* 107: 10314–10319.
- Ricklefs RE, Scheuerlein A (2001) Comparison of aging-related mortality among birds and mammals. *Experimental gerontology* 36: 845–857.

- Rodríguez-Robles JA, Thomas R (1992) Venom function in the Puerto Rican racer, *Alsophis portoricensis* (Serpentes: Colubridae). *Copeia* pp. 62–68.
- Rohlf FJ (2001) Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* 55: 2143–2160.
- Rubene D, Håstad O, Tauson R, Wall H, Ödeen A (2010) The presence of UV wavelengths improves the temporal resolution of the avian visual system. *The Journal of experimental biology* 213: 3357–3363.
- Sato K, Watanuki Y, Takahashi A, Miller PJ, Tanaka H, et al. (2007) Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proceedings of the Royal Society B: Biological Sciences* 274: 471–477.
- Schoch RM (1985) Preliminary description of a new late Paleocene land-mammal fauna from South Carolina, USA. Peabody Museum of Natural History, Yale University.
- Schwartz SH, Meese T (2010) Visual perception: A clinical orientation. McGraw-Hill Medical Pub. Division.
- Shattuck MR, Williams SA (2010) Arboreality has allowed for the evolution of increased longevity in mammals. *Proceedings of the National Academy of Sciences* 107: 4635–4639.
- Shine R, Schwaner T (1985) Prey constriction by venomous snakes: a review, and new data on Australian species. *Copeia* pp. 1067–1071.
- Sibly RM, Brown JH, Kodric-Brown A (2012) Metabolic ecology: a scaling approach. John Wiley & Sons.
- Stearns SC (1992) The evolution of life histories, vol. 249. Oxford University Press Oxford.
- Stevens M (2007) Predator perception and the interrelation between different forms of protective coloration. *Proceedings of the Royal Society B: Biological Sciences* 274: 1457–1464.
- Tacutu R, Craig T, Budovsky A, Wuttke D, Lehmann G, et al. (2012) Human ageing genomic resources: integrated databases and tools for the biology and genetics of ageing. *Nucleic acids research* p. gks1155.
- Tansley K, et al. (1965) Vision in vertebrates. *Vision in vertebrates* .

- Tatler B, O'Carroll D, Laughlin S (2000) Temperature and the temporal resolving power of fly photoreceptors. *Journal of Comparative Physiology A* 186: 399–407.
- Therrien F, Henderson DM (2007) My theropod is bigger than yoursâ€ or not: estimating body size from skull length in theropods. *Journal of Vertebrate Paleontology* 27: 108–115.
- Tosh CR, Ruxton GD (2010) Modelling perception with artificial neural networks. Cambridge University Press.
- Vogel S (2008) Modes and scaling in aquatic locomotion. *Integrative and Comparative Biology* 48: 702–712.
- Vonk FJ, Casewell NR, Henkel CV, Heimberg AM, Jansen HJ, et al. (2013) The king cobra genome reveals dynamic gene evolution and adaptation in the snake venom system. *Proceedings of the National Academy of Sciences* 110: 20651–20656.
- Voris HK, Moffett MW (1981) Size and proportion relationship between the beaked sea snake and its prey. *Biotropica* pp. 15–19.
- Voss RS (2013) Opossums (Mammalia: Didelphidae) in the diets of Neotropical pitvipers (Serpentes: Crotalinae): Evidence for alternative coevolutionary outcomes? *Toxicon* 66: 1–6.
- Watanabe YY, Lydersen C, Fisk AT, Kovacs KM (2012) The slowest fish: swim speed and tail-beat frequency of Greenland sharks. *Journal of Experimental Marine Biology and Ecology* 426: 5–11.
- Wegner NC, Snodgrass OE, Dewar H, Hyde JR (2015) Whole-body endothermy in a mesopelagic fish, the opah, *Lampris guttatus*. *Science* 348: 786–789, URL <http://www.sciencemag.org/content/348/6236/786.abstract>.
- West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276: 122–126.
- White CR, Phillips NF, Seymour RS (2006) The scaling and temperature dependence of vertebrate metabolism. *Biology Letters* 2: 125–127.
- Widder EA (2010) Bioluminescence in the ocean: origins of biological, chemical, and ecological diversity. *Science* 328: 704–708.
- Wiens JJ, Brandley MC, Reeder TW (2006) Why does a trait evolve multiple times within a clade? Repeated evolution of snakeline body form in squamate reptiles. *Evolution* 60: 123–141.

- Wilkinson GS, South JM (2002) Life history, ecology and longevity in bats. *Aging cell* 1: 124–131.
- Williams GC (1957) Pleiotropy, Natural Selection, and the Evolution of Senescence. *Evolution* 11: pp. 398–411, URL <http://www.jstor.org/stable/2406060>.
- Williams SA, Shattuck MR (2015) Ecology, longevity and naked mole-rats: confounding effects of sociality? *Proceedings of the Royal Society of London B: Biological Sciences* 282: 20141664.
- Williams T, Wilson R, Boersma P, Stokes D (1995) The penguins, Spheniscidae. *Bird families of the world* (2) Show all parts in this series .
- Williams V, White J, Schwaner T, Sparrow A (1988) Variation in venom proteins from isolated populations of tiger snakes (*Notechis ater niger*, *N. scutatus*) in South Australia. *Toxicon* 26: 1067–1075.
- Wilson DE, Reeder DM (2005) Mammal species of the world: a taxonomic and geographic reference, vol. 1. JHU Press.
- Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, et al. (2005) Body size in ecological networks. *Trends in Ecology & Evolution* 20: 402–409, URL <http://www.sciencedirect.com/science/article/pii/S0169534705000893>.
- Zhang G, Cowled C, Shi Z, Huang Z, Bishop-Lilly KA, et al. (2013) Comparative analysis of bat genomes provides insight into the evolution of flight and immunity. *Science* 339: 456–460.

## APPENDIX A

### SUPPLEMENTARY INFORMATION TO CHAPTER 2

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#### A.1 PHYLOGENY RECONSTRUCTION

Divergence times and phylogenies from the literature were used to produce a composite phylogeny of the vertebrate species used in our analyses (Figure 2.2). For species with no available divergence dates based on molecular data or available published trees, conservatively estimated first appearance dates from the Paleobiology database (PBDB) were used as an estimate of divergence time (Alroy et al., 2008). Divergence dates for the major groups Batoidea, Actinopterygii and Amphibia were taken from the TimeTree database (Hedges et al., 2006). For divergence dates of Carcharhinus and Sphyna Lim et al. (2010) was used, while the divergence time between *Negaprion brevirostris* and *Carcharchinus acronotus* was estimated based on the first appearance in the fossil record of *Negaprion brevirostris*, the younger of the two species (*Negaprion* spp - 40.3mya, *Carcharchinus* - 46.2). Li et al. (2008) were used to infer phylogenetic relationships and divergence times in Actinopterygii, and Little et al. (2010) was used for perciform divergence times. For divergence time between anapsids (turtles and birds) and suarapids (Squamata and Sphenodon) the estimation from Benton and Donoghue (2007) was used while Perelman et al. (2011) was used for the divergence and phylogenetic relationships among Squamata, Sphenodon, turtles and Aves. For divergence times within the Squamata Wiens et al. (2006) was used, while for turtle species I used Naro-Maciel et al. (2008). I used Brown et al. (2008) for the Aves phylogeny with divergence times between *Asio flammeus* and *Bubo virginianus* estimated using an estimate of the first appearance (Jánossy, 2011). (Murphy et al., 2007) was used for divergence dates of mammalian orders, while for primates I used Perelman et al. (2011). Rodent divergence times were taken from Murphy et al. (2007).

## A.2 SENSITIVITY ANALYSES

A series of sensitivity analyses was performed to test if the results of the main analysis were affected by (1) the temperature that ectoderm species metabolic rates were corrected to, (2) the inclusion of brain mass as a control for information processing abilities and (3) the quality of the data used in the analysis.

### A.2.1 *Ectotherm temperature sensitivity*

I used Q10 values, the fold change in metabolic rate over a temperature change of 10°C, as defined for each of the major groups (i.e. reptilian, amphibian etc; See Methods in main text) to correct ectotherm mass specific metabolism ( $qWg$ ) over a temperature range of 5°C to 35°C. This analysis was performed by re-running the main analysis with  $qWg$  corrected to 5°C and then corrected to 35°C. The resulting set of models and the terms which they included are given in Tables S2 and S3. In both analyses the model with the lowest AIC includes the same terms as found in the main analysis, i.e., body mass (Mg), temperature corrected mass-specific resting metabolic rate ( $qWg$ ) and light levels, with qualitatively the same significant affects (Tables S6 and S7).

TABLE. Coefficients of the model with all factors included. Mg = body mass (grams),  $qWg$  = Temperature corrected mass-specific resting metabolic rate  $Wg-1$ , Light.l (low) = effect of low light levels on CFF in comparison to high light levels, exp = effect of experimental type (ERG = electroretinogram) in comparison to behavior based CFF measures.

Variable	Estimate	S.E	t-value	P-value
Intercept	141.48	15.15	9.34	$4^{-10}$
Mg	-4.40	2.01	-2.18	0.038
$qWg$	16.89	4.31	3.92	$5^{-4}$
Light levels (low)	-37.74	5.94	-6.36	$7^{-7}$
Measurement type (exp)	-3.66	6.24	-0.59	0.56
Data quality (high)	-3.86	6.14	-0.63	0.53
Lambda (Low)	Mode 0	Lower 95% C.I 0	Upper 95% C.I 0.34	$R^2 = 0.69$

### A.2.2 *Brain Mass analysis*

As the amount of sensory tissue available to an organism may aid in its ability to perceive and process information, brain mass values, measured as wet weight

TABLE. Coefficients of the model with all factors included. Mg = body mass (grams), qWg = Temperature corrected mass-specific resting metabolic rate Wg-1, Light.l (low) = effect of low light levels on CFF in comparison to high light levels, exp = effect of experimental type (ERG = electroretinogram) in comparison to behavior based CFF measures.

<i>Variable</i>	<i>Estimate</i>	<i>S.E</i>	<i>t-value</i>	<i>P-value</i>
Intercept	141.48	15.15	9.34	$4^{-10}$
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qWg	16.89	4.31	3.92	$5^{-4}$
Light levels (low)	-37.74	5.94	-6.36	$7^{-7}$
Measurement type (exp)	-3.66	6.24	-0.59	0.56
Data quality (high)	-3.86	6.14	-0.63	0.53
Lambda (Low)	Mode 0	Lower 95% C.I. 0	Upper 95% C.I. 0.34	
				$R^2 = 0.69$

(g), were taken from the literature (Table 1, Methods). As data on brain mass was available for only a subset of twenty-eight species, the term brain mass was included along with the terms used in the main analysis (light levels, qWg, experimental design and body mass) in a series of models performed on the restricted data set (Table S4). While a similar trend to the first analysis was found, a positive effect of mass specific resting metabolic rate () and negative effects of low light levels () and body mass (), brain mass was found to have no significant effect on CFF levels ().

TABLE. Coefficients of the model with all factors included. Mg = body mass (grams), qWg = Temperature corrected mass-specific resting metabolic rate Wg-1, Light.l (low) = effect of low light levels on CFF in comparison to high light levels, exp = effect of experimental type (ERG = electroretinogram) in comparison to behavior based CFF measures.

<i>Variable</i>	<i>Estimate</i>	<i>S.E</i>	<i>t-value</i>	<i>P-value</i>
Intercept	141.48	15.15	9.34	$4^{-10}$
Mg	-4.40	2.01	-2.18	0.038
qWg	16.89	4.31	3.92	$5^{-4}$
Light levels (low)	-37.74	5.94	-6.36	$7^{-7}$
Measurement type (exp)	-3.66	6.24	-0.59	0.56
Data quality (high)	-3.86	6.14	-0.63	0.53
Lambda (Low)	Mode 0	Lower 95% C.I. 0	Upper 95% C.I. 0.34	
				$R^2 = 0.69$

## APPENDIX B

# SUPPLEMENTARY INFORMATION TO CHAPTER 3

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## B.1 ADDITIONAL DETAILS OF DATA COLLECTION AND SOURCES

### B.1.1 *Flight capability*

Species were categorised as either volant, non-volant or gliders. Most birds, apart from ratites, penguins and some flightless rails, are volant. All mammals apart from bats are non-volant. We classed mammals as gliders if they regularly use gliding as a means of locomotion and have adaptations that aid their descent e.g., skin flaps.

### B.1.2 *Activity period*

Most animals will be active to some extent at both day and night. Therefore activity period was define using the times when a species is feeding/foraging as this is when they are most likely to be exposed to predation. For example, many bats often fly around their roosts during the day but only leave their roosts to feed at night; therefore such species are classed as nocturnal. We defined species as diurnal, nocturnal, crepuscular or cathemeral by looking for the following key phrases in the literature:

- **Diurnal:** diurnal, active in the day, mainly/predominantly/mostly/generally diurnal or active in the day, crepuscular and diurnal or active in the day, diurnal or active in the day and sometimes/occasionally/infrequently/rarely diurnal or active in the day.
- **Nocturnal:** nocturnal, active at night, mainly/predominantly/mostly/generally nocturnal or active at night, crepuscular and nocturnal or active at night, nocturnal or active at night and sometimes/occasionally/infrequently/rarely diurnal or active in the day.
- **Crepuscular:** crepuscular, active at dusk and dawn, active early morning and evening (not afternoon). Note that crepuscular and diurnal animals are classed as diurnal; crepuscular and nocturnal animals are classed as nocturnal

- **Cathemeral:** cathemeral, diurnal and nocturnal, active any time of the day or night, nocturnal and often/frequently diurnal or active in the day, diurnal and often/frequently nocturnal or active at night.

In cases where none of the above keywords were present activity pattern was also defined if all other alternatives could be ruled out, for example species with roosting behaviour described as beginning before sunset and ending only after sunrise can be described as diurnal as it excludes nocturnal, cathemeral and crepuscular daily activity feeding patterns.

#### B.1.3 *Foraging environment*

Foraging environments were defined as terrestrial, semi-arboreal, arboreal, aerial or aquatic, by looking for the following key phrases in the literature:

- **Terrestrial:** terrestrial, feeds at ground-level (including rocky areas), mainly/predominantly/mostly/feeds at ground-level, feeds at ground-level and sometimes/occasionally/infrequently/rarely feeds above ground-level.
- **Arboreal:** arboreal, feeds at above ground-level (including trees), mainly/predominantly/mostly/feeds at ground-level, feeds at ground-level and sometimes/occasionally/infrequently/rarely feeds above ground-level.
- **Semi-arboreal:** semi-arboreal, semi-terrestrial, feeds at above ground-level and at ground-level, feeds at ground-level and often/frequently feeds at above ground-level, feeds at above ground-level and often/frequently feeds at ground-level.
- **Aerial:** volant, feeds while flying, mainly/predominantly/mostly/generally aerial forager, aerial forager and sometimes/occasionally/infrequently/rarely feeds at ground-level or above ground-level. Includes insectivorous bats and birds.
- **Aquatic:** aquatic, feeds in water, mainly/predominantly/mostly/generally feeds in water, feeds in water and sometimes/occasionally/infrequently/rarely feeds at ground-level or above ground-level. Includes marine birds, ducks, seals and otters. If feeds in both terrestrial and aquatic environments counted as terrestrial.

### B.1.4 *Fossoriality*

Species were defined as either fossorial, non-fossorial or semi-fossorial by looking for the following key phrases in the literature:

- **Fossorial:** fossorial, lives in burrows and rarely leaves them, mainly/predominantly/mostly fossorial, fossorial and sometimes/occasionally/infrequently active above ground.
- **Non-fossorial:** non-fossorial, terrestrial, mainly/predominantly/mostly/generally terrestrial or non-fossorial, terrestrial or non-fossorial and sometimes/occasionally/infrequently burrows, may excavate shallow scrapes but nothing useful for predator defense, incapable of excavating burrows.
- **Semi-fossorial:** semi-fossorial, lives in burrows and leaves them frequently, fossorial and often/frequently active above ground, non-fossorial and often/frequently uses burrows, capable of excavating burrows.

### B.1.5 *Chronogram calibration diagnosis*

Following the recommendations of Parham et al. (2011), our chronogram calibration used the following fossil:

Taxa: *Archerpeton anthracos*

Holotype: RM 12056

Author: Carroll 1964

Phylogeny: (Reisz and Müller, 2004)

Epoch: Westphalian A (Canada Nova Scotia)

Age: 318.1 - 314.6 Myr

Dating: International Commission on Stratigraphy 2009

## B.2 SUPPLEMENTARY TABLES

TABLE. Breakdown of numbers of species in each category included in the analyses. Values under the Sample column represent the number of species with 100 or more available longevity studies. Values under the BMR column represent the number of species with available basal metabolic rate (BMR) data.

Category*		Volant			Non-volant			Total		
		Full	Sample	BMR	Full	Sample	BMR	Full	Sample	BMR
<b>Foraging environment</b>	-Terrestrial	235	199	58	494	257	223	729	456	281
	-Arboreal	120	83	12	115	61	35	235	144	47
	-Semi-Arboreal	96	72	23	76	44	36	172	116	59
	-Aerial	111	92	35	NA	NA	0	111	92	35
<b>Activity pattern</b>	-Aquatic	105	90	19	16	11	6	121	101	25
	-Diurnal	451	361	84	206	139	62	657	500	146
	-Nocturnal	117	95	44	335	133	163	452	228	207
<b>Fossoriality</b>	-Cathemeral	78	65	15	115	70	58	193	135	73
	-Crepuscular	16	15	4	50	31	17	66	46	21
	-Fossorial	0	0	0	10	5	7	10	5	7
	-Semi-fossorial	10	9	3	209	77	131	219	86	134
	-Non-fossorial	652	527	144	487	291	162	1139	818	306
<b>Total</b>		<b>662</b>	<b>536</b>	<b>147</b>	<b>706</b>	<b>373</b>	<b>300</b>	<b>1368</b>	<b>909</b>	<b>447</b>

TABLE. Table B2: Relationship between maximum longevity (years), body mass (g) and flight capability (volant or non-volant) in 909 species of birds and mammals with over 100 maximum lifespan records.

Fixed Terms	Estimate ( $\beta$ )	Lower CI	Upper CI	Posterior distribution
<b>Intercept</b>	-0.194	-1.466	1.079	
<b>Body Mass</b>	0.551	0.444	0.658	
<b>Flight capability - Volant</b>	0.855	0.316	1.401	
<b>Body Mass: Flight capability</b>	0.477	0.305	0.652	
<b>Random Terms</b>				
<b>Residual variance</b>	0.130	0.107	0.156	
<b>Phylogenetic variance</b>	1.222	0.934	1.598	

Notes: 18000000 iterations with 3000000 burnin and thinning interval of 75000.

TABLE. Table B3: Relationship between maximum longevity (years), body mass (g), foraging environment and activity period, in 536 species of volant birds and mammals with over 100 samples of longevity.

Fixed Terms	Estimate ( $\beta$ )	Lower CI	Upper CI	Posterior distribution
<b>Intercept</b>	0.749	-0.549	2.040	
<b>Body Mass</b>	1.039	0.891	1.187	
<b>Foraging environment</b>	- Aerial	0.073	-0.197	
	- Arboreal	0.017	-0.203	
	- Semi-arboreal	0.125	-0.087	
	- Aquatic	-0.188	-0.422	
<b>Activity period</b>	- Cathemeral	0.152	-0.043	
	- Crepuscular	-0.502	-0.811	
	- Nocturnal	-0.100	-0.380	
<b>Random Terms</b>				
<b>Residual variance</b>	0.202	0.163	0.249	
<b>Phylogenetic variance</b>	1.046	0.677	1.612	

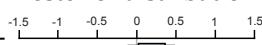
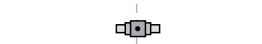
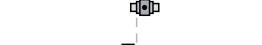
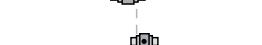
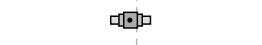
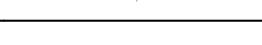
Notes: 12000000 iterations with 2000000 burnin and thinning interval of 5000.

TABLE. Table B4: Relationship between maximum longevity (years), body mass (g), foraging environment, fossoriality and activity period, in 373 species of nonvolant birds and mammals with over 100 samples of longevity.

<b>Fixed Terms</b>		<b>Estimate (<math>\beta</math>)</b>	<b>Lower CI</b>	<b>Upper CI</b>	<b>Posterior distribution</b>
<b>Intercept</b>		-0.045	-1.222	1.158	
<b>Body Mass</b>		0.542	0.455	0.629	
<b>Foraging environment</b>	- Arboreal	0.293	0.117	0.468	
	- Semi-arboreal	0.125	-0.015	0.265	
	- Aquatic	0.081	-0.209	0.376	
<b>Fossoriality</b>	- Fossorial	-0.522	0.134	0.915	
	- Semi-fossorial	-0.048	-0.190	0.095	
<b>Activity period</b>	- Cathemeral	0.028	-0.086	0.141	
	- Crepuscular	-0.087	-0.231	0.057	
	- Nocturnal	0.116	-0.004	0.237	
<b>Random Terms</b>					
<b>Residual variance</b>		0.036	0.025	0.051	
<b>Phylogenetic variance</b>		1.040	0.792	1.366	

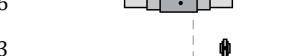
Notes: 18000000 iterations with 3000000 burnin and thinning interval of 7500.

TABLE. Relationship between maximum longevity (years), body mass (g), foraging environment and activity period in 589 birds.

Fixed Terms	Estimate ( $\beta$ )	Lower CI	Upper CI	Posterior distribution
<b>Intercept</b>	0.192	-0.353	0.676	
<b>Body Mass</b>	1.025	0.889	1.164	
<b>Foraging environment</b>	- Aerial	0.017	-0.258	
	- Arboreal	0.040	-0.151	
	- Semi-arboreal	0.100	-0.075	
	- Aquatic	-0.110	-0.329	
<b>Activity period</b>	- Cathemeral	0.100	-0.714	
	- Crepuscular	-0.444	-0.749	
	- Nocturnal	-0.077	-0.330	
<b>Random Terms</b>				
<b>Residual variance</b>	0.181	0.147	0.222	
<b>Phylogenetic variance</b>	0.371	0.245	0.579	

Notes: 18000000 iterations with 3000000 burnin and thinning interval of 7500.

TABLE. Relationship between maximum longevity (years), body mass (g), foraging environment, fossoriality, and activity period 779 mammals..

<b>Fixed Terms</b>		<b>Estimate (<math>\beta</math>)</b>	<b>Lower CI</b>	<b>Upper CI</b>	<b>Posterior distribution</b>
<b>Intercept</b>		-0.248	-1.166	0.666	
<b>Body Mass</b>		0.540	0.458	0.623	
<b>Foraging environment</b>	- Aerial	0.411	0.085	0.740	
	- Arboreal	0.233	0.084	0.381	
	- Semi arboreal	0.151	0.019	0.285	
	- Aquatic	-0.067	-0.347	0.209	
<b>Fossoriality</b>	- Fossorial	0.423	0.054	0.789	
	- Semi-fossorial	0.022	-0.099	0.144	
<b>Activity period</b>	- Cathemeral	0.051	-0.071	0.175	
	- Crepuscular	-0.063	-0.217	0.090	
	- Nocturnal	0.029	-0.092	0.151	
<b>Random Terms</b>					
<b>Residual variance</b>		0.051	0.038	0.071	
<b>Phylogenetic variance</b>		0.936	0.753	1.146	

Notes: 18000000 iterations with 3000000 burnin and thinning interval of 7500.