

PREDATOR-PREY INTERACTIONS ACROSS SCALE AND DIMENSIONALITY

by

KEVIN HEALY

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DECLARATION

I declare that this thesis has not been submitted as an exercise for a degree at this or any other university and it is, unless otherwise referenced, entirely my own work. I agree to deposit this thesis in the University's open access institutional repository or allow the library to do so on my behalf, subject to Irish Copyright Legislation and Trinity College Library conditions of use and acknowledgement.

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SUMMARY

Predator-prey interactions are an important evolutionary driver of species form and diversity, 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 better and more general ecological predictions. In this thesis I explore the role of two fundamental components of predator-prey interactions: the body size of both predators and their prey and the dimensionality of the interactions between them. 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

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 ran 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, 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 additional analysis showing that including the error associated with phylogeny construction further strengthens the association between of eusociality and increased lifespan.

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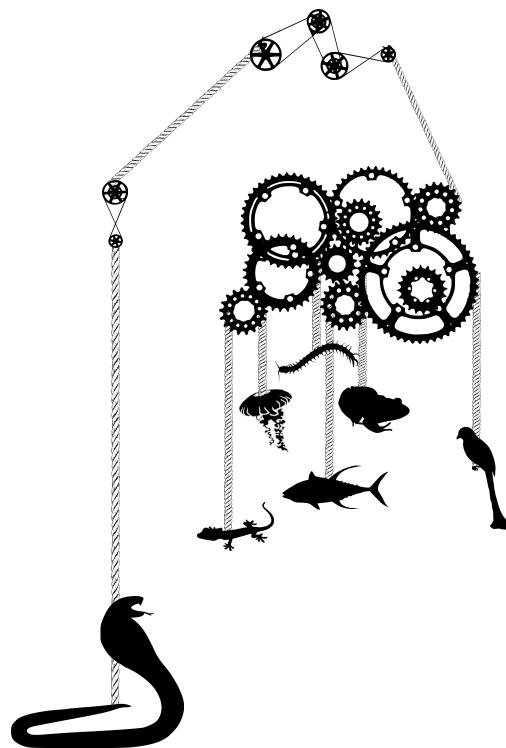
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CHAPTER 1

GENERAL INTRODUCTION



“It is interesting to contemplate a tangled bank...”

Charles Darwin

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 environments and ecosystems, each predator-prey interaction plays out within its own specific context. For example, two predators may rely on two different strategies to capture the same prey, such as relying on venom or manoeuvrability,

despite being similar in size and form. However, amongst these context dependences, certain patterns emerge that provide a clear approach to understand how these interactions emerge and affect 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 due to buoyancy (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 their link with both body size and the dimensionality of these interactions (Figure 1.).

Since Kleiber fist demonstrated the link between the rate of energy utilised by an animal and its size (Kleiber, 1947), ecologists have utilised this correlation to understand a range of biological processes and principles (Sibly et al., 2012; West et al., 1997; Brown et al., 2004). 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 surrounding the exact nature of this scaling and the fundamental basis that underpins it (Isaac and Carbone, 2010), 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 interactions play out in has more recently gained attention as a key component.

Similar to the formalisation of metabolic theory in the mid 90s, 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) were the first to use this geometry to describe how the space filling properties of vegetation can determine arthropod community densities through habitat availability. This approach of defining dimensionality using fractals has been used to determine the effects of dimensionality across numerous ecological systems (Kenkel and Walker, 1996; Shorrocks et al., 1991; Gunnarsson, 1992; Gee and Warwick, 1994; Jeffries, 1993) and used as a general approach to define ecological structure (Cohen, 1995; Henderson and

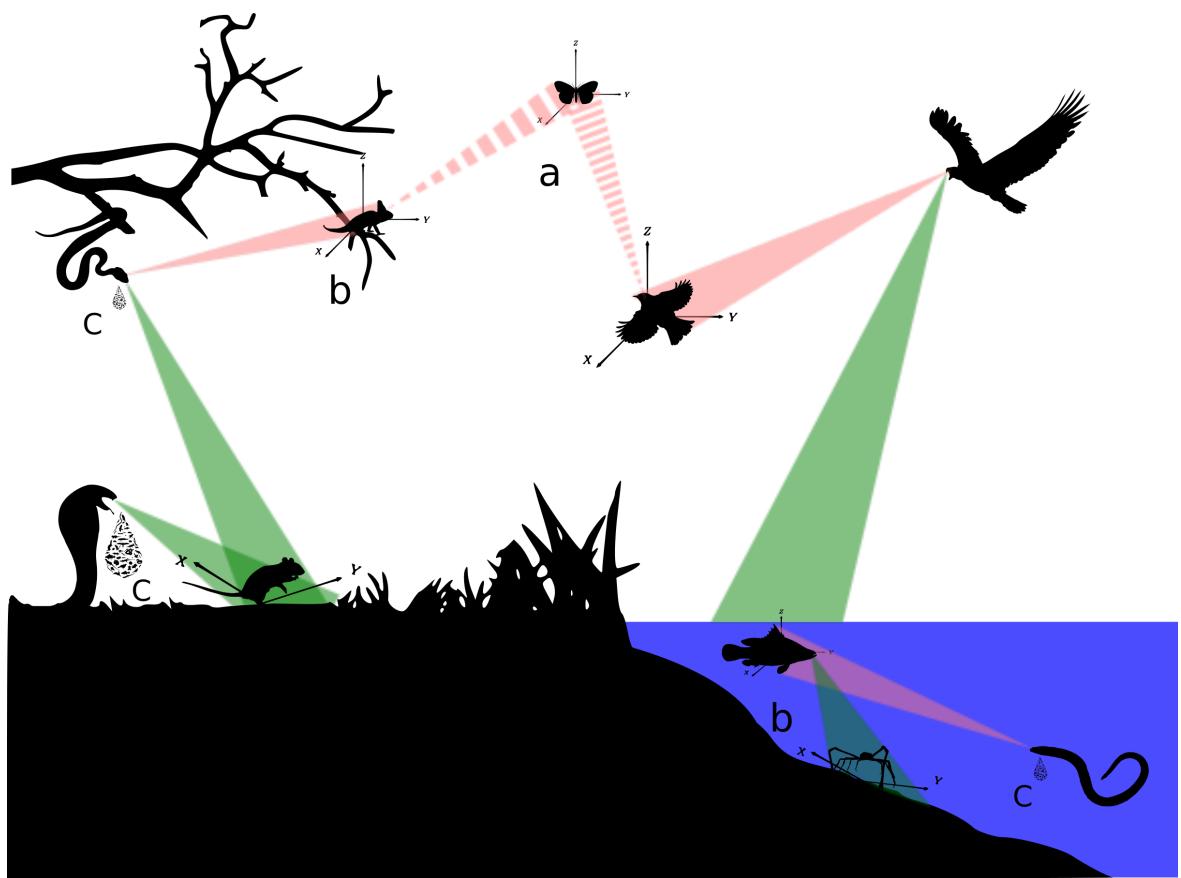


FIGURE 1.1: If a species searches across a habitat surface, such as a terrestrial or water surface, the interaction can be defined as 2D (Green cones). If a species searches across a volume, such as pelagic or aerial environments, the interaction can be defined as 3D (Red cones). As arboreal habitats display the space filling properties of an object with a dimensionality higher than a two dimensional object, searching such volumes would also constitute high dimensional interactions. The dimensionality of the environment a species resides within is also likely to influence its ability to escape. Species in high dimensional habitats, such as pelagic, arboreal and aerial environments, have more routes of escape in comparison to species in low dimensional habitats such as terrestrial and benthic habitats. Interactions are also dependent on the ability of species to sample the temporal dimension with high temporal resolution allowing for more accurate tracking of predator or prey movements. This thesis explores several factors associated with interaction dimensionality including; a. The link between temporal perception, body size and metabolic rate; b. How escape space may affect life-history evolution; c. how the dimensionality of the habitat may affect predator traits evolution, in particular venom.

Magurran, 2010). More recently however, the focus of dimensionality has shifted from that of the habitat to that of the interactions themselves.

While species may be associated with habitats of different dimensions, for example the two dimensions of terrestrial systems or the three dimensions of open pelagic systems, the interaction dimensionality mainly depends on where the prey species resides. For example, a bird may be within a 3D aerial environment while flying, but is effectively foraging over a 2D habitat (Figure 1). Such a bird would hence

experience the foraging limitations of two dimensional space but also the predation pressures and escape strategies associated with existing within three dimensions (Pawar et al., 2012). This framework allows dimensionality to be explored across groups and foraging strategies and extends the predictive ability of body mass scaling through incorporating the difference in the scaling of interaction rates across interaction dimensionality. It also opens up the importance of the role of sensory ecology within such interactions, in particular as such sensory systems may show different scaling in comparison to that predicted from metabolic theory (McGill and Mittelbach, 2006; Kiltie, 2000).

This thesis draws on how both body size and dimensionality, two aspects that intersect physics and biology, affect predator-prey interactions across the range of contexts these predator-prey 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 or more physiologically capable to process temporal information 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 the need for small size and a high metabolic rate.

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_{50}), diets, body size, environment dimensionality and both maximum and minimum venom volumes comprising of 101 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 general prey-specific nature of venom toxicity using phylogenetic distance between diet species and LD_{50} model species as a test. I discuss the possible mechanisms and the implications of these results in relation to both the evolution of venom and costly predatory traits in general.

Finally, in **Chapter 5**, I close with a discussion of the importance of including dimensionality in macroecological models and the future methodologies and directions relating to the research presented in this thesis.

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.

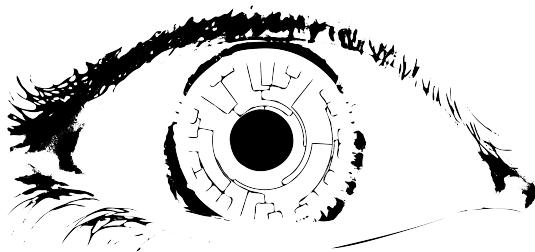
I was involved with the conception, data analysis and write-up of this paper.

Kane, A., Ruxton, G.D., Jackson, A.L. & Healy, K.(2015). Body size drives importance of scavenging in theropods. Submitted to *The American Naturalist*.

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

CHAPTER 2

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



“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 find support for this hypothesis across a wide range of vertebrates. 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; Kiltie, 2000). The limitations such sensory systems are constrained by can determine ecological interactions through, for example, predation and mate selection where the abilities of the parties involved to capture, escape or be seduced is dependent on how they perceive their environment (Fig. 2.1; 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 environment are relatively well studied (Cronin, 2005; Clark et al., 2012), how they perceive the 4th dimension, time, is less well known.

As the environment is fundamentally dynamic in nature, the ability to integrate information over a time period is a necessity for any organism. 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

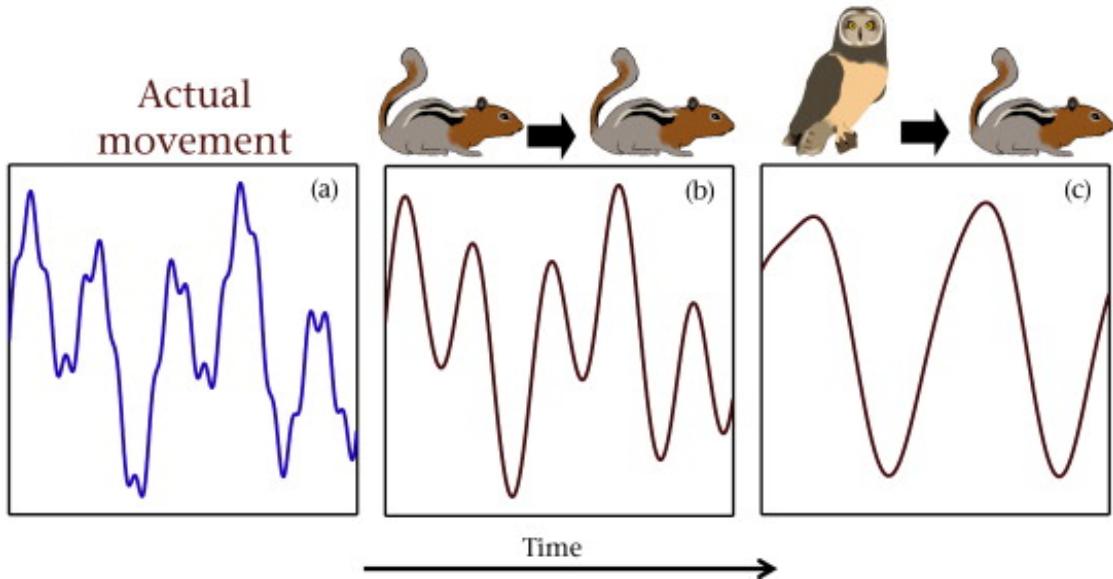


FIGURE 2.1: The ability of an organism to track a moving object depends on the time integral over which the individual can obtain its information. This is determined by its ability to resolve temporal information. In cases where an animal, such as a ground squirrel, displays complex movement (a), conspecifics 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 were collated from the literature (Table ??). 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 FishBase (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; Table 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 rest-

ing 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.

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.1 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 °C and 35 °C (see Appendix A.2.1). 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.2.2).

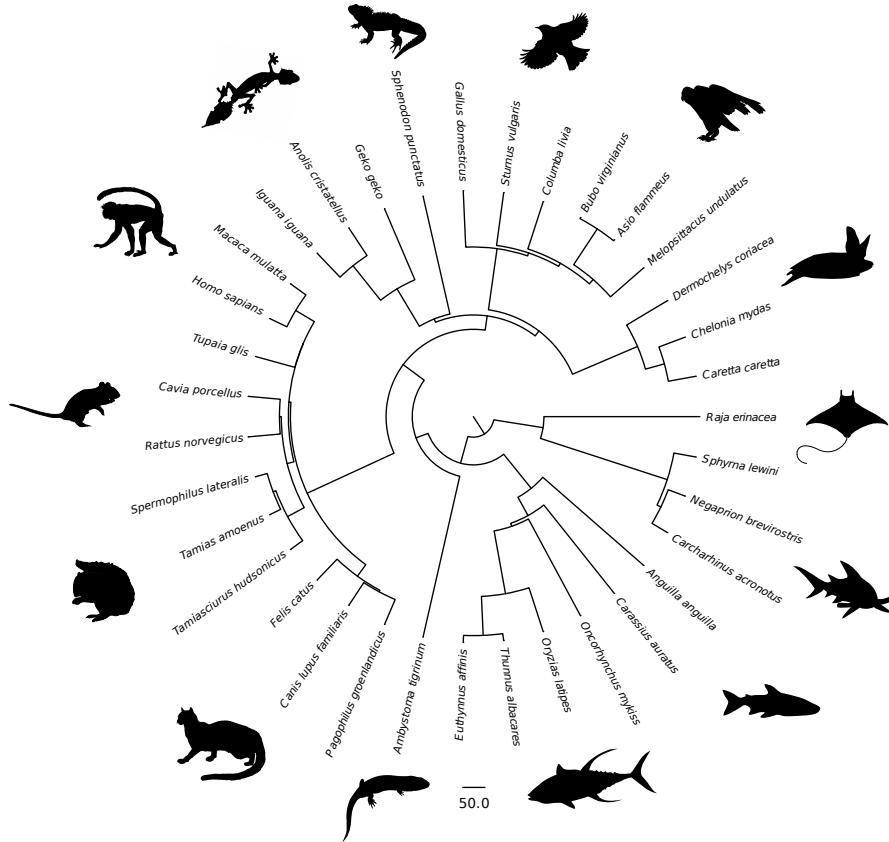


FIGURE 2.2: Phylogeny of species used in analysis. Scale bar represents million of years. See appendix A for divergence times.

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 2.1).

2.3.2 Statistical Analyses

To test the hypothesis that small species with high metabolic rates show the highest CFF values, 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 (λ), 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

TABLE 2.1: Data used in the analysis including, maximum critical flicker fusion (CFF), Mass in grams (Mg), mass specific resting metabolic rate corrected to 20 °C in ectotherms (qWg), Brain Mass in grams, Light levels (L = low, H = High)

Species	CFF	Mg	qWg	Brain Mass	Light levels
<i>Ambystoma tigrinums</i>	30 ^{e,s,1}	10.78 ²⁸	0.00016 ²⁸	NA	L
<i>Anguilla anguilla</i>	14 ^{b,s,2}	71.1 ²⁸	0.00013 ²⁸	NA	L
<i>Anolis cristatellus</i>	70 ^{e,o,3}	6.0 ²⁹	0.00089 ²⁹	NA	H
<i>Asio flammeus</i>	70 ^{e,o,4}	406.0 ³⁰	0.0032 ²⁸	5.45 ⁶⁹	H
<i>Bubo virginianus</i>	45 ^{e,s,5}	1450.0 ³¹	0.0036 ²⁸	13.7 ⁷⁰	L
<i>Canis lupus familiaris</i>	80 ^{b,s,6}	13900.0 ³²	0.00183 ²⁸	80.0 ⁷¹	H
<i>Carassius auratus</i>	67.2 ^{e,o,7}	10.8 ³³	0.00013 ²⁸	0.01 ⁷¹	H
<i>Carcharhinus acronotus</i>	18 ^{e,o,8}	14491.0 ⁸	0.00114 ^{56*}	NA	L
<i>Caretta caretta</i>	40 ^{e,s,9}	135000.0 ³⁴	0.00008 ⁵⁷	2.7 ⁴⁰	H
<i>Cavia porcellus</i>	50 ^{e,s,10}	629.0 ³⁵	0.00306 ³⁵	3.8 ⁷²	L
<i>Chelonia mydas</i>	40 ^{e,s,9}	128000.0 ³⁶	0.00025 ³⁶	8.6 ⁷¹	H
<i>Columba livia</i>	100 ^{e,s,4}	315.0 ³⁷	0.0045 ²⁸	2.3 ⁷⁰	H
<i>Dermochelys coriacea</i>	15 ^{e,s,11}	354000.0 ³⁸	0.00043 ⁵⁸	30.0 ⁷³	H
<i>Felis catus</i>	55 ^{e,s,12}	3054.4 ³²	0.00394 ⁵⁹	28.4 ⁷¹	L
<i>Gallus gallus domesticus</i>	87 ^{b,o,13}	2710.0 ³⁹	0.0022 ²⁸	3.6 ⁷⁴	H
<i>Gekko gecko</i>	20 ^{e,s,14}	54.8 ⁴⁰	0.00034 ²⁸	0.2 ⁷⁵	L
<i>Homo sapiens</i>	60 ^{b,o,15}	67100.0 ⁴¹	0.00117 ⁶⁰	1300.0 ⁷⁶	H
<i>Iguana iguana</i>	80 ^{e,s,14}	750.0 ⁴²	0.00029 ²⁸	0.61 ⁷⁵	H
<i>Macaca mulatta</i>	95 ^{b,o,16}	7710.0 ⁴³	0.00205 ⁶¹	91.7 ⁷¹	H
<i>Melopsittacus undulatus</i>	74.7 ^{b,s,17}	33.6 ²⁸	0.01204 ²⁸	1.5 ⁷⁰	H
<i>Negaprion brevirostris</i>	37 ^{e,s,18}	92987.0 ⁴⁴	0.00053 ^{62*}	NA	L
<i>Oncorhynchus mykiss</i>	27 ^{b,s,19}	4000.0 ⁴⁵	0.00041 ²⁸	0.5 ⁷¹	L
<i>Oryzias latipes</i>	37.2 ^{e,s,20}	0.21 ²⁰	0.00072 ²⁸	0.01 ⁷⁷	L
<i>Pagophilus groenlandicus</i>	32.7 ^{b,s,12}	119600.0 ⁴⁶	0.00211 ⁶³	228.5 ⁷⁸	L
<i>Raja erinacea</i>	30 ^{e,o,22}	500.0 ⁴⁷	0.00024 ⁴⁷	2.32 ⁷¹	L
<i>Rattus norvegicus</i>	39 ^{e,o,23}	237.0 ⁴⁸	0.00679 ⁴⁸	2.3 ⁷⁹	L
<i>Spermophilus lateralis</i>	120 ^{e,o,10}	215.5 ⁴⁹	0.00335 ⁶⁴	3.6 ⁸⁰	H
<i>Sphenodon punctatus</i>	45.6 ^{b,s,24}	353.75 ⁵⁰	0.00017 ²⁸	NA	L
<i>Sphyrana lewini</i>	27.3 ^{e,o,8}	1893.0 ^{8,51}	0.0010 ^{65*}	60.0 ⁷⁷	L
<i>Sturnus vulgaris</i>	100 ^{e,s,25}	75.0 ²⁸	0.012 ²⁸	1.9 ⁷⁴	H
<i>Tamias amoenus</i>	100 ^{e,o,10}	51.91 ⁵²	0.00937 ⁶⁶	1.98 ⁸⁰	H
<i>Tamiasciurus hudsonicus</i>	60 ^{e,o,10}	215 ³⁵	0.00735 ⁶⁷	4.0 ⁸⁰	H
<i>Thunnus albacares</i>	80 ^{e,s,26}	45349.0 ^{53,54}	0.00158 ^{68*}	6.24 ⁷⁷	H
<i>Tupaia glis</i>	90 ^{b,o,27}	142.0 ⁵⁵	0.00424 ⁵⁵	3.4 ⁷⁹	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°C) mass specific resting metabolic rate (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) Bornschein & 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) Graber (1962); (31) Ganey et al. (1993); (32) Kendall et al. (1982); (33) Hughes et al. (1977); (34) Duermitt (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 & and Lavigne (1984); (47) Howe & 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) Iwanicki & Nelson (2002); (71)

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).

2.4 RESULTS

In the main analysis body mass had a negative effect on the temporal resolution of the sensory system (Table 2.2, Figure 2.3a), while metabolic rate, after correcting for mass and temperature, was positively associated with CFF (Table 2.2, Figure 2.3b) and low environmental light levels were associated with an overall reduction in CFF (Table 2.2, Figure 2.3). Phylogeny was found to have a minimal effect on the resulting models ($\lambda = 0$, Table 2) and experimental type was not correlated with CFF (Table 2.2). 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.

TABLE 2.2: 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 behaviour based CFF measures.

Variable	Estimate	S.E	t-value	P-value
Intercept	141.48	15.15	9.34	4×10^{-10}
Mg	-4.40	2.01	-2.18	0.038
qWg	16.89	4.31	3.92	5×10^{-4}
Light levels (low)	-37.74	5.94	-6.36	7×10^{-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	$R^2 = 0.69$

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) showing the same trends as found in the main analysis (Appendix A.2.1). 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 (Appendix A.2.2).

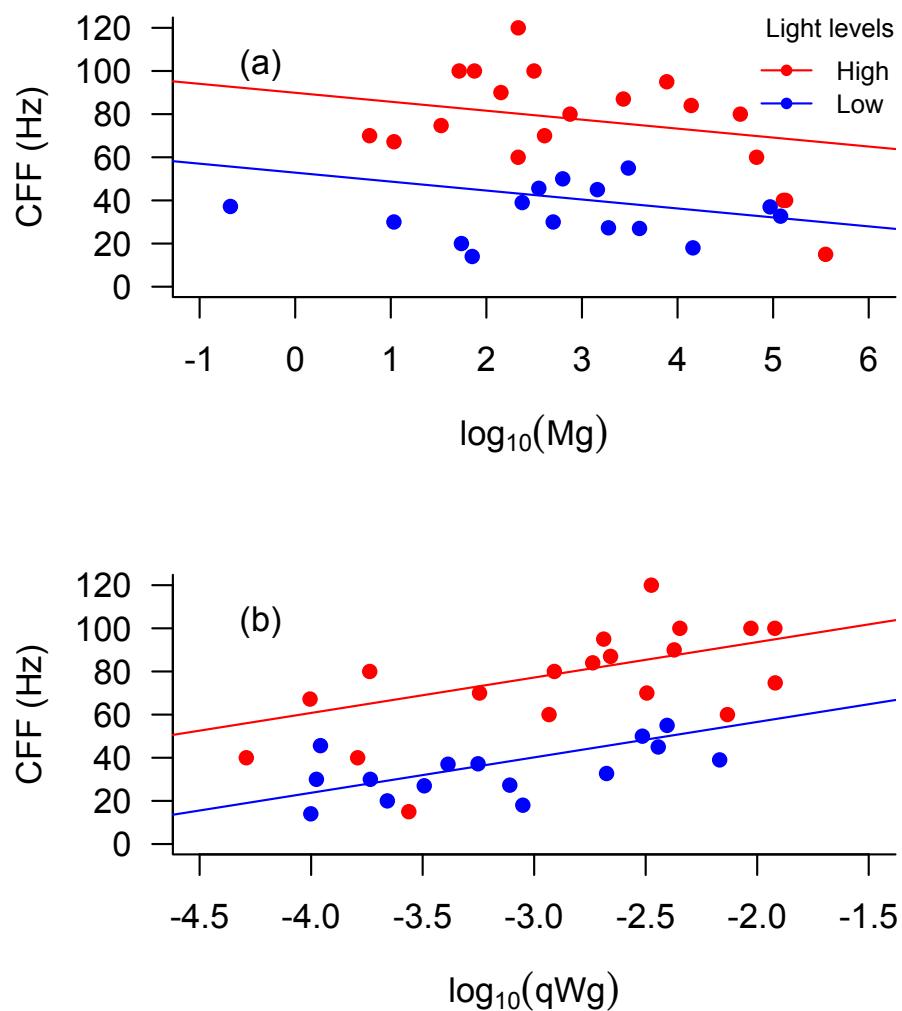


FIGURE 2.3: The effect of \log_{10} body mass, light levels and \log_{10} temperature corrected mass-specific resting metabolic rate (qWg) on critical flicker fusion frequency (CFF). The minimal adequate model (Results) indicates CFF increases with $\log_{10} qWg$ but decreases with body mass. Low light levels (blue) are associated with low CFF values in comparison to high light levels (red).

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 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 metabolic rate (Laughlin, 2001). It is unsurprising hence that species which have high metabolisms also benefit from an increase 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 the case in the visual system of the deep sea escolar which has one of the lowest temporal perception of any vertebrate (Landgren et al., 2014). This reduction of investment in temporal perception 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 supported by research showing that faster and more manoeuvrable fly species have higher temporal resolutions (Laughlin and Weckström, 1993) and that less manoeuvrable species of scavenger crabs display slower response 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 size predatory swordfish are capable of a ten-fold increase in their CFF, levels expected of a small endotherm in this model, through specialised heating tissues in thier eyes (Fritsches et al., 2005). This is achieved through this specialised tissue increasing the temperature, and hence the metabolic rate, in their visual systems allowing them to up-regulate 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; Wegner et al., 2015) 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).

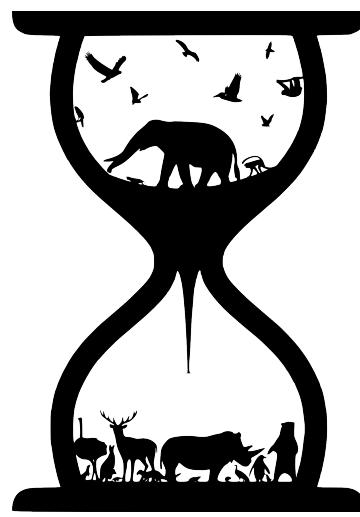
The effects of body size and metabolic rate on temporal resolution and the presence of sensory adaptations also point towards an interesting axis of niche space. Disparity in size and metabolic rate among species within an ecological setting may select for particular sets of adaptations creating a diverse 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 an axis 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 are perceived as flasing lures by the target 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 realised 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 metabolism and 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



“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 allow for 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 the ability to fly (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 volancy, 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 effects on species' life-history evolution.

3.2 INTRODUCTION

Lifespan, or longevity, is a fundamental life-history trait that exhibits considerable variation both within and across 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 compared to 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

(Hossie et al., 2013), show increased lifespans. 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 increased 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 additional 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 with other ecological factors may also likely to play a role in life-history evolution. 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 these 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 those restricted to singular habitats; (iii) 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 (iv) 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 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 was 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 captive individuals are expected to live longer than wild individuals, on average maximum longevity tends to remain unchanged between captive and wild populations (Ricklefs and Scheuerlein, 2001).

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. (2012) for birds and excluded purely aquatic mammals (Cetacea and Sirenia) from the analyses because selection pressures would be expected to be very different in these groups. Gliding mammals were also excluded because there were too few species 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 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 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. All data is available with the corresponding paper (Healy et al., 2014).

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, nu = 1, the prior mean alpha.mu = 0, and 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 distribution.

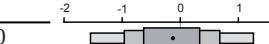
To determine whether the conclusions held when species with fewer than 100 longevity records were excluded, models 1-3 were repeated with the reduced dataset of species with 100 or more longevity records. I also repeated Models 2 and 3 for birds and mammals (rather than volant and non-volant species) 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 hierarchical 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. All code is available as part of the *mulTree* package (Guillerme and Healy, 2014).

3.4 RESULTS

The analysis show that volant species live longer than non-volant species of a similar body mass (Table 3.1, Figure 3.1). 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 3.1) increase significantly more than the lifespans of non-volant species (modal slope estimate [after converting from mean-centred values] = 0.13; Table 3.1).

TABLE 3.1: 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% credibility interval from 500 models. Upper CI = Upper 95% credibility 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 (β)	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.

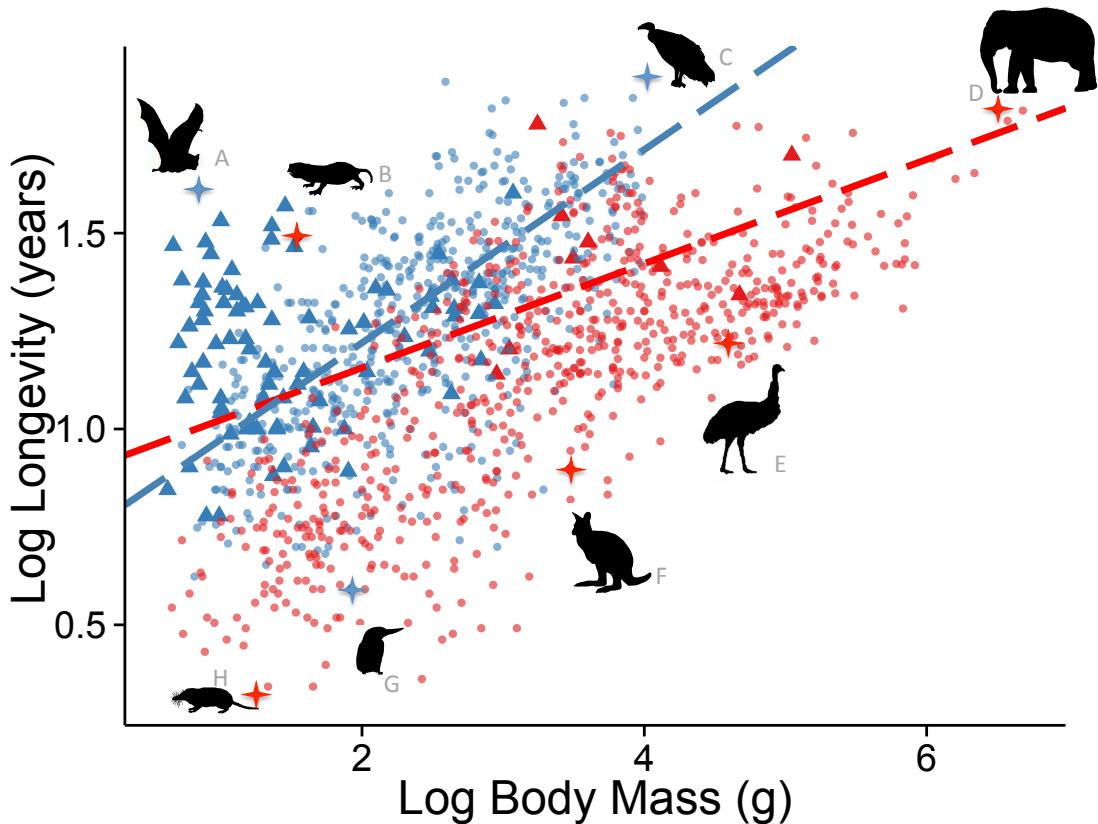


FIGURE 3.1: Relationships between body mass and maximum lifespan in birds and mammals. Silhouettes highlight a selection of species with much longer or shorter lifespans than expected given their body size. These species are (A) *Myotis brandtii*, Brandt's bat; (B) *Heterocephalus glaber*, Naked mole 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 3.1.

TABLE 3.2: 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% credibility interval from 500 models. Upper CI = Upper 95% credibility interval from 500 models. Posterior distribution = distribution of estimates from 500 models.

Fixed Terms		Estimate (β)	Lower CI	Upper CI	Posterior distribution
Intercept		0.668	-0.664	2.028	
Body Mass		1.035	0.899	1.172	
Foraging environment	- Aerial	0.116	-0.119	0.354	
	- Arboreal	0.068	-0.119	0.258	
	- Semi-arboreal	0.124	-0.056	0.301	
	- Aquatic	-0.166	-0.383	0.049	
Activity period	- Cathemeral	0.085	-0.088	0.261	
	- Crepuscular	-0.479	-0.772	-0.182	
	- Nocturnal	-0.131	-0.385	0.122	
<hr/>					
Random Terms					
Residual variance		0.184	0.151	0.223	
Phylogenetic variance		1.155	0.789	1.693	

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

TABLE 3.3: Table 3. 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% credibility interval from 500 models. Upper CI = Upper 95% credibility interval from 500 models. Posterior distribution = distribution of estimates from 500 models.

Fixed Terms		Estimate (β)	Lower CI	Upper CI	Posterior distribution
Intercept		0.013	-1.433	1.467	
Body Mass		0.531	0.449	0.614	
Foraging environment	- Arboreal	0.213	0.070	0.358	
	- Semi-arboreal	0.148	0.022	0.274	
	- Aquatic	0.064	-0.220	0.341	
	- Fossorial	0.437	0.088	0.785	
Fossoriality	- Semi-fossorial	0.035	-0.081	0.149	
	- Cathemeral	0.060	-0.056	0.173	
	- Crepuscular	-0.050	-0.194	0.096	
	- Nocturnal	0.038	-0.075	0.153	
<hr/>					
Random Terms					
Residual variance		0.042	0.031	0.059	
Phylogenetic variance		1.627	1.319	1.985	

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

The relationships among the 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 3.2). In contrast, activity period was not associated with lifespan in non-volant species (Table 3.3). 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 3.2). Within non-volant species, however, those foraging arboreally have longer lifespans than those foraging terrestrially, while fossorial (i.e. burrowing) species live longer than non-fossorial ones (Table 3.3).

TABLE 3.4: 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% credibility interval from 25 models. Upper CI = Upper 95% credibility interval from 25 models. Posterior distribution = distribution of estimates from 25 models.

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

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

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; Tables 3.1-3.3) 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). Finally, the additional analysis of the dataset from Williams and Shattuck (2015) showed that eusociality but not fossoriality (as defined to include both semi-fossorial and fully fossorial species) increased maximum lifespan in small mammals (Table 3.4).

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 South, 2002) while among mammals, bats live far longer than similarly sized non-volant mammals (Wilkinson and South, 2002; Austad and Fischer, 1991). 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 of 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 known extinct predatory 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 relatively predator free existence of large flying species such as found in the longest living volant species in our dataset the Andean condor *Vultur gryphus*.

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). 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 following Williams and Shattuck (2015) subsequent analysis here 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 reduced 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 and life history evolution within birds and mammals. However the biomechanical limitations associated with volancy and arboerality, 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, volancy, arboreality and eusociality is clear, the direct causal link between these factors 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 analyses 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.

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

Aldous Huxley



4.1 SUMMARY

The evolution of venom in snakes offers a distinctive system of predator-prey interactions of ecological, evolutionary and medical interest. Despite this many fundamental questions regarding the evolution of this trait still persist, such as the perplexing range in the toxicity and quantities of venom found across species. For example, despite the obvious benefits of possessing venom, many species have either entirely lost or have extremely low venom volumes and toxicities. One of the potential answers to this paradox are the costs associated with replenishing large amounts of venom, in particular in species where venom is surplus to the requirement of capturing prey. Here I test several hypotheses relating to the ecological factors that may be associated with the atrophy of venom in snakes including diet, body size

and habitat dimensionality. 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 101 species of venomous snakes. I find that species associated with high dimensional habitats and a diet of eggs show atrophy of venom through reduced venom volumes and in the case of oviparity, reduced toxicity. These results also show that, despite predictions, levels of toxicity show no association with the volume of venom produced by a species. However snake venom was found to be prey-specific with venoms tested on prey models closely related to the diet of the focal species showing higher levels of toxicity. Overall snake venom provides a remarkable story 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 the reduction and eventual loss of limbs 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 venom cocktails (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 costly predatory traits and predator-prey interactions.

Snake venoms rely on a complex of proteins and other compounds to create neurotoxic and hemotoxic affects in their target prey (Greene, 1997; Casewell et al., 2013). While the biological properties these mixtures possess has led to a wide body of biomedical research, there is surprisingly little understanding of the ecological pressures associated with the evolution of venoms 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 of 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 a role in prey acquisition a more likely primary function (Casewell et al., 2013). 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 is seen at its most extreme vestigial state in the marbled sea snake *Aipysurus eydouxii*, which despite being a member of one of the most venomous groups of snakes, is incapable of even delivering the residual amounts of venom still found in its vestigial glands (Li et al., 2005). While not all snakes show such extreme levels of atrophy, intermediate levels of reduced venom volumes and toxicities can be found across diverse groups of snakes (Fry et al., 2012). One possible solution to this paradox is the investment cost associated with venom replenishment.

Venom synthesis carries a cost both with regards to the energy requirements of venom production and the lost opportunities while replenishing such venom. After venom extraction pit-vipers have been shown to greatly increase their metabolic rates over a 72 hour period McCue (2006). Also, although other species show lower metabolic costs associated with producing venom (Pintor et al., 2010), species that are heavily dependent on their venom to capture prey would also suffer lost opportunities over the replenishment period (Young et al., 2002). For example *Bitis arietans* requires at least seven days to fully restock its venom glands (Currier et al., 2012). This cost of venom replenishment is also 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 may explain the case of *Aipysurus eydouxii*, where a switch to an egg-based diet is likely to be the driver of venom loss due to the removal of the need to incapacitate their prey (Li et al., 2005). However many species do include eggs within their diet (de Queiroz and Rodríguez-Robles, 2006) yet 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 snake species 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 snake venoms that correlate with diet (Daltry et al., 1996). However, the presence

of such prey specificity in venom is not clear 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. For example ground squirrels show resistance to the venom of their rattlesnake predators (Poran et al., 1987), and there is evidence that resistance to pit viper venoms in opossums has led to a switch in predator-prey roles with opossums now the predators of pit vipers (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, in order to keep pace with prey resistance (Vonk et al., 2013). Such evolutionary events are likely to be relatively rare (Vonk et al., 2013), which may result in species relying on increased venom doses in order to overcome prey resistance in the short term. Species with 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 (Sasa, 1999; Mebs, 2001). 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 snake's natural prey (da Silva and Aird, 2001). A more realistic interpretation of the data requires including the physiological distance such test species may have in comparison to the snake's diet, with species that have 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, expected encounter rates with such prey may also be an important determinant in the volume and toxicity of a snake's venom.

While incapacitating prey is a primary function of venom, venom evolution might also be expected to be influenced by the probability of encountering prey. One such aspect which may influence these probabilities is habitat dimensionality. As encounter rates show higher scaling with body mass in high dimensional interactions, such as expected in arboreal and aquatic snakes, investment in venom production

may be decreased due to the higher probability of encountering prey which would reduce the costs associated with failed predation attempts. High dimensionality may also reduce venom volumes in order to increase replenishment rates which would allow species to fully exploit such increased encounter rates. In particular arboreal species show faster digestion rates than terrestrial species hence increased replenishing rates may be strongly selected in these 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 (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 of venom available to a species, size, diet and environment I test the relationship between venom toxicity and both the maximum and mean volume of venom available snake species. 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 different levels of venom volume and toxicity.

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, where lower values of LD_{50} indicate a higher venom toxicity (Chippaux et al., 1991). As the route of inoculation can affect LD_{50} (Chippaux et al., 1991) 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 mouse 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 is likely to represent the most costly component to produce. In the case of multiple estimates from different studies the mean values across the studies, were used as the value for that species with the maximum across all studies

used as the overall maximum value. When available, data on sub species was included as a separate measure as venoms can show large variations across sub species (Chippaux et al., 1991).

Diet data was collated from the literature using studies with quantitative estimates of prey proportions, mainly from studies of stomach contents. 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 LD₅₀ test species had higher toxicities I calculated a score of the phylogenetic distance between the LD₅₀ test species 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 LD₅₀ 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 LD₅₀ 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 $Mass(g) = 0.00035(Total\ Length(cm))^{3.02}$ from Pough (1980).

Mass, LD₅₀, 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 4.1).

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

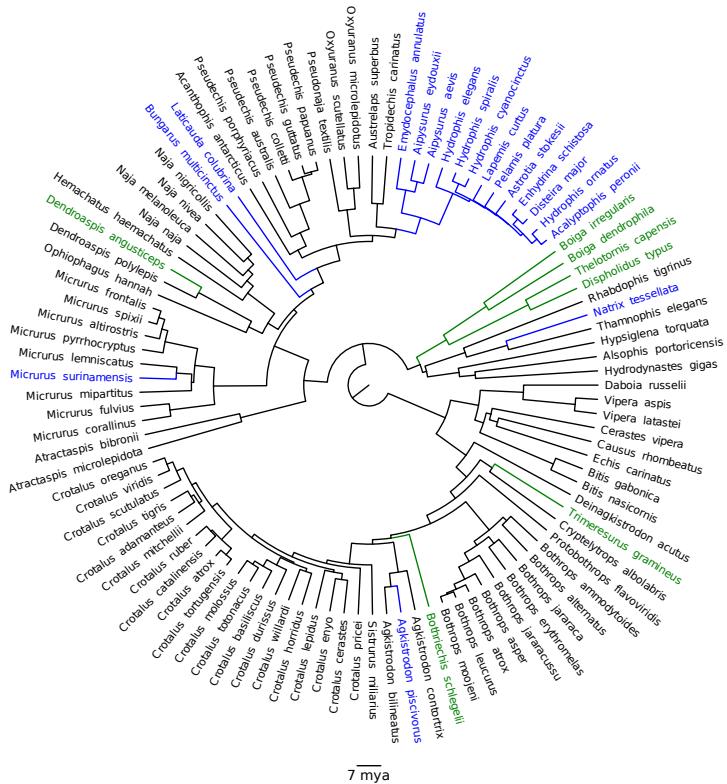


FIGURE 4.1: Phylogeny of species used in analysis. Scale bar represents million of years. Species coloured blue are aquatic, species coloured green are arboreal and species coloured black are terrestrial or fossorial.

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 LD₅₀ are likely to have co-evolved, both were included as response variables (allowing for covariance between them to be estimated) with mass, LD₅₀ inoculation method, habitat dimensionality, the presence of eggs in diet and phylogenetic distance from LD₅₀ 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 as a random term using the MCMCglmm package (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 which exceeded 1000 for all parameter estimates and convergence tested using the Gelman-Rubin statistic (Gelman and Rubin, 1992).

4.4 RESULTS

After controlling for phylogeny these analyses showed that smaller species that inhabit high dimensional environments have both lower mean and maximum volumes of venom (Figures 4.2a and 4.2b, Tables 4.2 and 4.5). Toxicity was affected by the route of inoculation, with intravenous and intrapulmonary inoculation routes showing lower LD₅₀ in comparison to subcutaneous measures, and the phylogenetic distance between the LD₅₀ model and species diet, with diets closer to the LD₅₀ model showing higher toxicities (Tables 4.3 and 4.6). Species with egg based diets showed a significant reduction in toxicity and maximum venom volume but not average venom volume (Tables 4.2, 4.3, 4.5, 4.6).

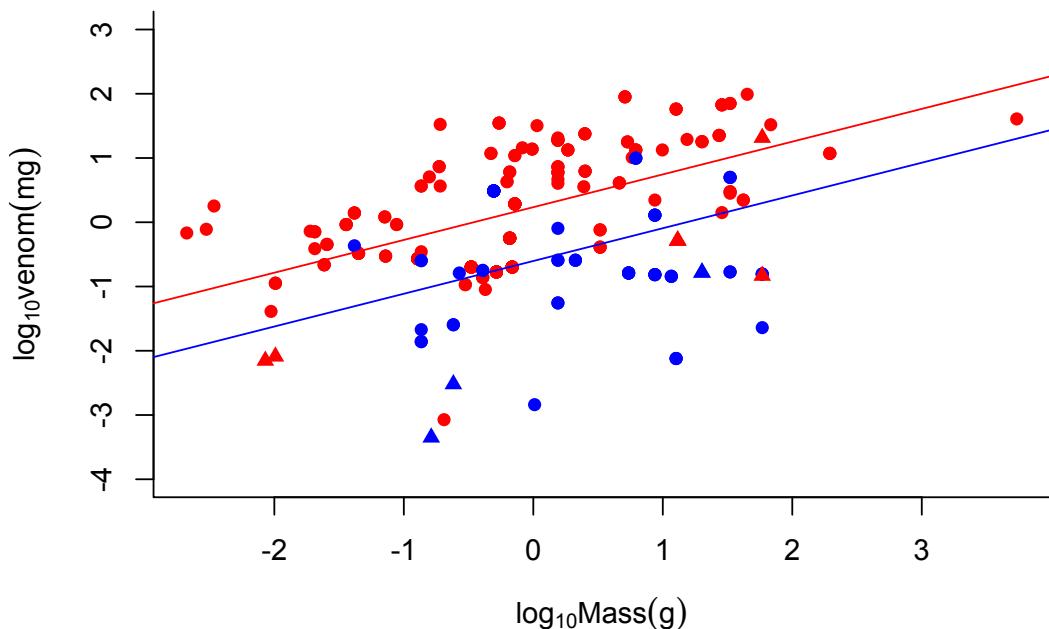


FIGURE 4.2: Log₁₀ Body size (g) against Log₁₀ mean venom volume (mg). Red points and line indicate species associated with low dimensional habitats. Blue points and line indicate species associated with high dimensional habitats. Triangles represent species with eggs found in their diet.

There was no correlation between LD₅₀ and either maximum or mean venom volumes (Tables 4.1 and 4.4). Both LD₅₀ and venom volume show high phylogenetic variance with phylogeny showing a higher association with LD₅₀ in comparison to venom volume in both models (Tables 4.1 and 4.4).

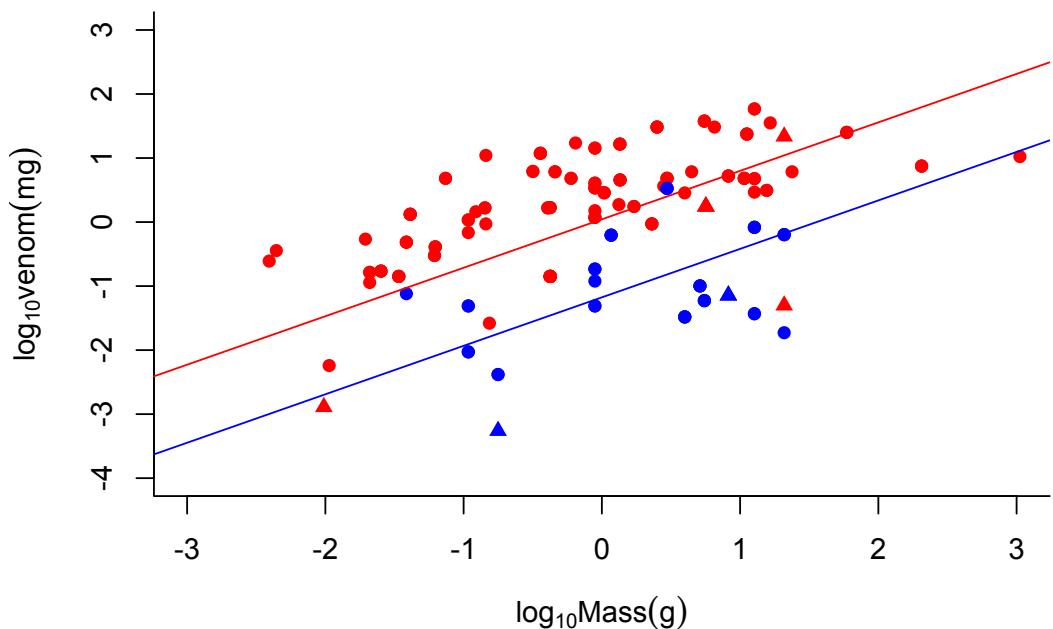


FIGURE 4.3: \log_{10} Body size (g) against \log_{10} maximum venom volume (mg). Red points and line indicate species associated with low dimensional habitats. Blue points and line indicate species associated with high dimensional habitats. Triangles represent species with eggs found in their diet.

TABLE 4.1: Variance Co-variance structure of random terms in the model using mean venom volumes. The variance associated with mean volume and LD₅₀ and the covariance between mean volume and LD₅₀ is given for the phylogenetic structure (Phylogeny), the residuals and a term to account for variation associated at the species and subspecies level (Species). Lower CI = lower 95% credibility interval, Upper CI = Upper 95% credibility interval.

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

TABLE 4.2: Relationship between average venom volume and body mass, inoculation method, habitat dimensionality, presence of eggs in diet and average phylogenetic distance between diet and LD₅₀ model. Lower CI = lower 95% credibility interval, Upper CI = Upper 95% credibility interval.

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

TABLE 4.3: Relationship between LD₅₀ and body mass, inoculation method, habitat dimensionality, presence of eggs in diet and average phylogenetic distance between diet and LD₅₀ model in average venom volume model. Lower CI = lower 95% credibility interval, Upper CI = Upper 95% credibility interval.

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

TABLE 4.4: Variance Co-variance structure of random terms in the model using maximum venom volumes. The variance associated with mean volume and LD₅₀ and the covariance between mean volume and LD₅₀ is given for the phylogenetic structure (Phylogeny), the residuals and a term to account for variation associated at the species and subspecies level (Species). Lower CI = lower 95% credibility interval, Upper CI = Upper 95% credibility interval.

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

TABLE 4.5: Relationship between maximum venom volume and body mass, inoculation method, habitat dimensionality, presence of eggs in diet and average phylogenetic distance between diet and LD₅₀ model. Lower CI = lower 95% credibility interval, Upper CI = Upper 95% credibility interval.

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

TABLE 4.6: Relationship between LD₅₀ and body mass, inoculation method, habitat dimensionality, presence of eggs in diet and average phylogenetic distance between diet and LD₅₀ model in maximum venom volume model. Lower CI = lower 95% credibility interval, Upper CI = Upper 95% credibility interval.

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

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 a reduction of venom volumes, and, in the case of maximum venom volume, the presence of eggs in their diet. This is likely due to the costs of producing venom (Pintor et al., 2010) outweighing the benefits associated with maintaining it.

One of the drivers behind such a 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 weaker selection to maintain the larger reservoirs of venom required to respond to the rarer event of encountering a prey item in a low dimensional environment. The biomechanical limitations of arboreal lifestyles is also suggested to lead 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 the size of predators in these environments would also restrict 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 habitat dimensionality, and hence interaction dimensionality, the mechanism behind this pattern requires further investigation.

The nature of a snake's 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) more likely to represent secondary benefits. However these results should be interpreted with caution due to the low number of oviparous species within the analysis (eight with only four having diets

consisting of greater than 20% eggs) 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; Daltry et al., 1996) 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 LD₅₀ 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 between venom evolution and prey resistance, 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 LD₅₀ may account for the underestimation of toxicity levels in some species (da Silva and Aird, 2001), 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 behaviour or constriction in order to incapacitate prey (Shine and Schwaner, 1985).

While volume and LD₅₀ 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, LD₅₀ 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 one of limitation in many species, in particular in rear-fanged groups (Kardong, 1982). However many rear-fanged snakes such as species of *Dispholidus* can contain venom volumes similar or in excess of many front-fanged species showing that this trait is not insurmountable in these groups (Kochva et al., 1980; Fry et al., 2008).

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

CHAPTER 5

DISCUSSION

5.1 CONSIDERING DIMENSIONALITY

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

Throughout this thesis I demonstrate 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 these dimensions can determine the nature of many biological interactions. This is reflected in the results of chapters 2-4 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 this living.

While this thesis focuses on how traits associated with predator-prey interactions (targeting, escaping or capturing) are affected by interaction dimensionality, these effects are likely to hold important consequences for larger ecological systems. For example, trophic interaction strengths are one of the main determinants of ecosystem stability (May, 1972; Pimm, 1984) with systems with different ratios of interaction dimensionalities likely to demonstrate different dynamic behaviour in response to stress and perturbation (Donohue et al., 2013). Likewise by including the dimensions over which species interact a better understanding of the diversity of species form may also be achieved. For example by acknowledging the importance of prey tracking in mesopelagic systems several species with unique physiologies to increase temporal perception have been discovered (Fritsches et al., 2005; Frank et al., 2012; Landgren et al., 2014) including the first case of true endothermy in a fish (Wegner et al., 2015).

Throughout this thesis comparative analyses provided the main tool to investigate the large scale macroecological patterns central to each chapter. However additional methods will be required to further investigate the importance of interaction dimensionality in future work. While each chapter has attempted to resolve some outstanding question within ecology and evolution they in turn raised many more questions. The future directions associated with these chapters hence include not only consolidating the results found here but also towards expanding the methodology, data and framework associated with predator-prey interactions.

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 2, to the inclusion of the error associated with phylogeny construction in Chapter 3, to the multiple response models used in the final chapter the increased complexity of these models was 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 the paper on temporal perception relating to chapter 2 (Healy et al., 2013) numerous studies on the sensory perceptual abilities of different species have appeared, in particular in ecological settings such as deep sea environments (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 with the additional data becoming available opening up the opportunity for more nuanced analysis between species ecologies and their temporal perceptual abilities. In particular paired data on the visual systems between paired predator and prey species would allow for the testing of the existence of arms races similar to that seen in snake venom evolution in chapter 4. Other interesting avenues to explore would be the existence of scaling in other sensory systems, including olfactory (Uchida and Mainen, 2003), auditory (Bar et al., 2015) and tactile (Braam, 2005). Echolocation is likely to be a particularly fruitful sense to study sensory limitations on predator-prey interactions (Bar et al., 2015), in particular through comparison of the use

of echolocation in species ranging in size 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, particularly as phylogeny topology is still not fully resolved in many groups (Jetz et al., 2012; Burleigh et al., 2015; Pyron and Burbrink, 2014) and as Bayesian generated phylogenies are becoming more available (Arnold et al., 2010; Jetz et al., 2012). The importance of using this approach was demonstrated in the difference results with regards to the methods used by Williams and Shattuck (2015) and those used in chapter 3 (Healy et al., 2014; Healy, 2015), were including the error associated within the phylogeny showed that eusociality but not fossoriality was the main driver of longevity within the data.

Irrespective of methodology, these result bring into question the importance of fossoriality in the evolution of longevity. As longevity itself may be causally linked to the evolution of eusociality, due to the requirement of multiple interactions between individuals before the benefits of eusociality can accrue (McNally, 2013), comparative analyses similar to chapter 3 in groups where the conflict between fossoriality and eusociality does not arise may help resolve this question. Reptiles and amphibians are two such groups which show species of varying degrees of fossoriality but are mainly solitary in nature. Another useful future direction using comparative analyses to understand lifespan evolution is to test whether other groups of species that can avail of high dimensional escape routes show similar differences in life-history traits found in chapter 3. Pelagic and benthic marine species may provide a good test case for this hypothesis with benthic species unable to avail of the 3D escape space of pelagic species and as aquatic species would not be subjective to the same size limitations found in arboreal and aerial species.

The final chapter is yet to be published however the need for further comparative analyses 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. Also following the association between species that are ovivorous and the atrophy of venom a larger analysis comparing the ecologies of venomous and completely non venomous species would help extend this finding. Furthermore a character reconstruction approach similar to that used

to infer the evolution of viviparity in snakes (Pyron and Burbrink, 2014) would further illustrate the atrophy of venom in species that no longer require it.

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 presently outside 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 (Tisue and Wilensky, 2004). 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 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, also need to be incorporated. Neural networks would provide one such solution by 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 parameterised within reality, making them an ideal half-way house between simulations and experimental approaches (Floreano and Keller, 2010). Furthermore, while used to study predator-prey interactions such robot systems inadvertently displayed behaviours associated with limitations of their temporal perceptual abilities (Floreano and Keller, 2010). 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 constrained to terrestrial systems with the aerial robofly (Lauder, 2001) and aquatic robofish (Faria et al., 2010) two examples of extending these approach to other environments.

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 also extended into investigating shoaling behaviour in response to shark and whale predation events by incorporating the simple behaviour rules of Couzin et al. (2002).

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.

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APPENDIX A

SUPPLEMENTARY INFORMATION TO CHAPTER 2

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 ??). For species with no available divergence dates based on molecular data or available published trees, conservatively estimated first appearance dates from the Paleobiology database 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 were performed to test if the results of the main analysis were affected by (1) the temperature that ectoderm species metabolic rates were corrected too, and (2) the inclusion of brain mass as a control for information processing abilities.

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. In both analyses the same trends were found with decreased CFF associated with body mass and light levels and increased CFF associated with metabolic rate. Measurement type was not found to affect CFF in either model (Tables A1 and A2).

TABLE A.1: Table A1. Coefficients of the model with all factors included and mass specific metabolic rate corrected to 5°C. 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	129.47	11.79	10.99	7.5×10^{-12}
Mg	-4.18	1.91	-2.18	0.037
qWg	12.96	3.13	4.15	3×10^{-4}
Light levels (low)	-37.25	5.62	-6.63	3×10^{-7}
Measurement type (exp)	-2.57	6.05	-0.42	0.68
Lambda (Low)	Mode 0	Lower 95% C.I 0	Upper 95% C.I 0.26	$R^2 = 0.71$

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 (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

TABLE A.2: Table A2. Coefficients of the model with all factors included and mass specific metabolic rate corrected to 35°C. 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	147.65	18.22	8.11	6×10^{-9}
Mg	-4.20	2.06	-2.03	0.05
qWg	20.55	6.21	3.31	3×10^{-3}
Light levels (low)	-37.11	6.11	-6.07	1×10^{-6}
Measurement type (exp)	-6.60	6.46	-1.02	0.32
Lambda (Low)	Mode 0	Lower 95% C.I. 0	Upper 95% C.I. 0.37	
				$R^2 = 0.66$

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 A3). While a similar trend to the first analysis was found, a positive effect of mass specific resting metabolic rate and negative effect of low light levels and body mass, brain mass was found to have no significant effect on CFF levels.

TABLE A.3: Table A3. Coefficients of analysis using the reduced dataset including brain mass. 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; Brain Mass (g).

<i>Variable</i>	<i>Estimate</i>	<i>S.E</i>	<i>t-value</i>	<i>P-value</i>
Intercept	120.30	1.27	9.47	5×10^{-9}
Mg	-1.6	3.96	-4.15	0.01
qWg	13.00	4.46	2.92	8×10^{-3}
Light levels (low)	-37.74	5.94	-6.36	7×10^{-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

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 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/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 B.1: Table B1. 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.

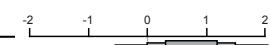
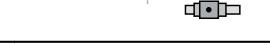
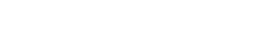
Category*		Volant		Non-volant		Total	
		Full	Sample	Full	Sample	Full	Sample
Foraging environment	-Terrestrial	235	199	494	257	729	456
	-Arboreal	120	83	115	61	235	144
	-Semi-Arboreal	96	72	76	44	172	116
	-Aerial	111	92	NA	NA	111	92
	-Aquatic	105	90	16	11	121	101
Activity pattern	-Diurnal	451	361	206	139	657	500
	-Nocturnal	117	95	335	133	452	228
	-Cathemeral	78	65	115	70	193	135
Fossoriality	-Crepuscular	16	15	50	31	66	46
	-Fossorial	0	0	10	5	10	5
	-Semi-fossorial	10	9	209	77	219	86
Total		662	536	706	373	1368	909

TABLE B.2: 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. Estimates are modal estimates from 500 models. Lower CI = Lower 95% credibility interval from 500 models. Upper CI = Upper 95% credibility interval from 500 models. Posterior distribution = distribution of estimates from 500 models.

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

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

TABLE B.3: 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. Estimates are modal estimates from 500 models. Lower CI = Lower 95% credibility interval from 500 models. Upper CI = Upper 95% credibility interval from 500 models. Posterior distribution = distribution of estimates from 500 models.

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

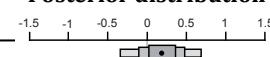
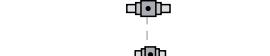
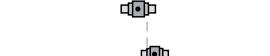
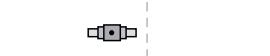
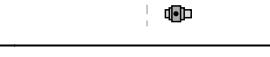
Notes: 12000000 iterations with 2000000 burnin and thinning interval of 5000.

TABLE B.4: 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. Estimates are modal estimates from 500 models. Lower CI = Lower 95% credibility interval from 500 models. Upper CI = Upper 95% credibility interval from 500 models. Posterior distribution = distribution of estimates from 500 models.

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

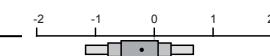
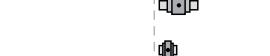
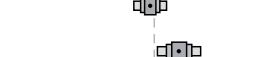
Notes: 18000000 iterations with 3000000 burnin and thinning interval of 7500.

TABLE B.5: Table B5: Relationship between maximum longevity (years), body mass (g), foraging environment and activity period in 589 birds. Estimates are modal estimates from 500 models. Lower CI = Lower 95% credibility interval from 500 models. Upper CI = Upper 95% credibility interval from 500 models. Posterior distribution = distribution of estimates from 500 models.

Fixed Terms		Estimate (β)	Lower CI	Upper CI	Posterior distribution
Intercept		0.192	-0.353	0.676	
Body Mass		1.025	0.889	1.164	
Foraging environment	- Aerial	0.017	-0.258	0.292	
	- Arboreal	0.040	-0.151	0.234	
	- Semi-arboreal	0.100	-0.075	0.281	
	- Aquatic	-0.110	-0.329	0.106	
Activity period	- Cathemeral	0.100	-0.714	0.271	
	- Crepuscular	-0.444	-0.749	-0.140	
	- Nocturnal	-0.077	-0.330	0.175	
<hr/>					
Random Terms					
Residual variance		0.181	0.147	0.222	
Phylogenetic variance		0.371	0.245	0.579	

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

TABLE B.6: Table B6: Relationship between maximum longevity (years), body mass (g), foraging environment, fossoriality, and activity period 779 mammals. Estimates are modal estimates from 500 models. Lower CI = Lower 95% credibility interval from 500 models. Upper CI = Upper 95% credibility interval from 500 models. Posterior distribution = distribution of estimates from 500 models.

Fixed Terms		Estimate (β)	Lower CI	Upper CI	Posterior distribution
Intercept		-0.248	-1.166	0.666	
Body Mass		0.540	0.458	0.623	
Foraging environment	- 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	
Fossoriality	- Fossorial	0.423	0.054	0.789	
	- Semi-fossorial	0.022	-0.099	0.144	
Activity period	- Cathemeral	0.051	-0.071	0.175	
	- Crepuscular	-0.063	-0.217	0.090	
	- Nocturnal	0.029	-0.092	0.151	
<hr/>					
Random Terms					
Residual variance		0.051	0.038	0.071	
Phylogenetic variance		0.936	0.753	1.146	

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