Metabolic physiology of Colubrid dietary specialists, *Dasypeltis scabra* and *Dasypeltis inornata*

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MASTER OF SCIENCE

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As the candidate's Supervisor I have approved this dissertation for submission:

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ABSTRACT

Metabolic rate (MR) and digestive duration are thermally dependant, and energy usage changes as body temperature (T_b) changes. Increased T_b during digestion causes a rapid increase in VO_2 and a shorter postprandial metabolic response known as specific dynamic action (SDA). SDA is the additional energy expended above standard metabolic rate (SMR) to carry out functions associated with meal digestion and assimilation. SDA is affected by prey size, prey type and body mass (M_b). Liquid meals require less energy to digest and assimilate than intact prey items resulting in a lower metabolic scope and reduced postprandial metabolic response. Digestive efficiency and metabolism are also affected by the level of dietary specialization which can lead to increased digestive efficiency in terms of duration and energy used for digesting preferred prey items. Here, I investigated the effects of M_b, T_b and ontogeny on standard and digestive MR of two dietary specialists, *Dasypeltis scabra* and *D. inornata*. *Dasypeltis scabra,* found throughout South Africa, and *D. inornata*, endemic to the eastern parts of South Africa and western part of Swaziland, digest only the liquid contents of freshly laid bird eggs and should have a lower energy cost of digestion and assimilation than other snake species consuming intact prey containing bones, fur or chitinous carapace. To test the effect of changes in T_b on the metabolic response of *Dasypeltis*, pre- and postprandial metabolic responses of adult *D. inornata* and adult and neonate *D. scabra* were compared. SMR and SDA were quantified at five ambient temperatures 20, 25, 27, 30, 32°C using closed system respirometry. SMR was measured for 3 days twice a day at 08h00 and 20h00. Thereafter, snakes were fed a meal of chicken egg equivalent to 20% of M_b and oxygen uptake (VO_2) was measured for an additional 5 days at 08h00 and 20h00, and then once a day at 08h00 for an additional 7 – 10 days. Increased T_b resulted in increases in metabolic response variables for all groups. Variation in T_b significantly affected SDA (kJ kg^{-1}) of *D. scabra* adults and neonates and *D. inornata* adults. There were few significant interspecific and ontogenetic differences across all temperature trials. Within five days after meal consumption for all groups at 32°C, postprandial VO_2 rates peaked at 3.16 - 3.73 times preprandial rates (scope), lower than most other snake species. The optimal digestion temperature appears to be around 32°C in terms of duration, but may be higher to optimize digestion. Across the range of temperatures (20 - 32°C) and masses (3.98 – 71.33g), the duration of significantly elevated VO_2 was on average 1.5 - 2 days longer for

D. scabra adults and neonates than *D. inornata*. Digestion duration ranged from 6.5 - 13.5 days for *D. inornata* and from 7.5 - 16.5 days for *D. scabra* adults and neonates. Digestive duration was longer for *D. scabra* than other snake species that consume meals of intact prey of similar size, at the same temperature. *Dasypeltis* species expended less total energy for digestion and used a smaller proportion of total energy consumed for digestion than other snake species at similar temperatures. Lower maintenance and digestive costs suggest that energy is conserved for allocation to other functions during periods of low prey availability. In addition, *Dasypeltis* species may rely on thermoregulation to capitalize on reduction in energy output and to increase energy savings between meals.

PREFACE

The experimental work described in this dissertation was carried out in the School of Biological and Conservation Sciences, Faculty of Science and Agriculture, University of KwaZulu-Natal, Pietermaritzburg from January 2007 to December 2009, under the supervision of Professor Michael R. Perrin and co-supervision of Dr. Suzanne McConnachie.

This dissertation submitted for the degree of Master of Science is the candidate's original work and has not been submitted, in part or in whole for a degree or diploma to any other university. Where use has been made of the work of others it is duly acknowledged in the text.

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Sara Greene Date

I certify that the above statement is correct.

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Professor Michael R. Perrin (Supervisor) Date

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Dr. Suzanne McConnachie (Co-Supervisor) Date

DECLARATION 1 – PLAGIARISM

I, SARA GREENE, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
5. Their words have been re-written but the general information attributed to them has been referenced
6. Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and referenced.

7. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, in press and published and give details of the contributions of each author to the experimental work and writing of each publication)

Publication 1 – **In preparation**

The effect of temperature, body mass and age on metabolic rate in the Colubrid dietary specialists, *Dasypeltis scabra* and *Dasypeltis inornata*.

Sara Greene, Michael R. Perrin, Suzanne McConnachie, Stephen Secor

Research was carried out by Sara Greene in fulfilment of MSc under the supervision of Professor Perrin and Dr. McConnachie. Experimental methods, equipment setup and statistical analysis advice were provided by Dr. Stephen Secor. Writing and corrections to the manuscript were contributed by all authors.

Signed:

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I must also give tremendous thanks to Dr. Stephen Secor for his guidance and advice with the technical and statistical aspects of this project. Thank you for your kindness and patience and for taking the time to help me even with your hectic schedule.

To my family – it has been a long journey, so far from you all, but your support never wavered. I love you. I miss you and from the bottom of my heart I thank you for believing in me. Mom and Dad - words cannot express my gratitude to you both. Allison – thank you for being a wonderful sister, inspiring me and making me realize why I needed to finish. To Mayo – no one knows what I went through with this project more than you. You encouraged me, you supported me through thick and thin, and you were there with me in the lab at all hours. You were always there for me in all aspects of this research, ensuring that I never gave up. You helped me more than you will ever know. Thank you so much. This is dedicated to Mayo and my family – without you this would not have been possible.

Thank you also to Caroline, Joe and Keri for assisting me with field work and turning over all those rocks. Snakes were obtained and transported under permission from Northwest Province Nature Conservation (Permit - 000222 NW-07). All research carried out at the University of KwaZulu-Natal was granted ethical clearance by the animal ethics sub-committee of the university under reference - 014/08/Animal.

TABLE OF CONTENTS

AUTHORS NOTE

Some repetition occurs between chapters, but was unavoidable as Chapter 2 is a manuscript in preparation for publication. Citations and the bibliography were formatted for the journal Physiological and Biochemical Zoology.

Chapter 1 – Literature Review

1.1 Introduction

In ectotherm physiology, various extrinsic and intrinsic factors such as environmental condition, photoperiod, circadian rhythm and the state of arousal/stress affect physiological systems (Cano and Nicieza 2006; de Souza et al. 2004; McDonald 1976; Peterson 1987; Stevenson et al. 1985). Temperature and metabolic rate are important factors that influence ecology and other biological functions (Angilletta et al. 2002b; Huey 1982; Skoczylas 1970). Metabolic rate is thermally sensitive (Lillywhite 1987), and changes in body temperature (T_b) can affect biochemical reaction rates (Seebacher and Franklin 2005). The highly labile nature of a reptile's T_b and the sensitivity of biochemical processes to changes in T_b suggest that some level of thermoregulation is critical to survival and performance (Blouin-Demers and Nadeau 2005; Cowles and Bogert 1944; Hardy 1979).

Reptilian T_b is affected by numerous factors linked to behavioural thermoregulation. These factors include reproductive state (Hutchison et al. 1966), thermoregulation differences between genders (Brown and Weatherhead 2000), thermal inertia related to body mass (M_b; Tanaka 2005), ecdysis vs. nonecdysis (McDonald 1976), digestive state (Stevenson et al. 1985), environmental factors (Christian and Bedford 1996) and season (Diaz 1997; Kiss et al. 2009). In turn, variation in T_b affects overall performance with respect to behavioural and physiological functions (Huey and Kingsolver 1989; Lillywhite 1987; Seebacher 2005). Locomotion (Cano and Nicieza 2006; Stevenson et al. 1985), metabolism and digestive efficiency (Greenwald and Kanter 1979; Regal 1966; Secor et al. 2007), juvenile mortality (Brown et al. 2004), foraging (Van Damme et al. 1991), growth (Andrews 1982; Angilletta 2001a) and total activity time (Melville and Swain 1997) are regulated by a reptile's ability to maintain T_b at or near an optimal level. Gender determination and hatchling success, while not directly regulated by T_b, are temperature dependent in some oviparous species during embryonic development (Janzen and Paukstis 1991) and can be affected by parental brooding which increases the incubation temperature (Hutchison et al. 1966).

The relationship between a reptile's T_b and performance is described by an asymmetric function known as a performance curve (Figure 1.1). Performance curves

illustrate the thermal sensitivity of a physiological process and the relative performance of the reptile over a range of T_b known as the performance breadth (Angilletta 2001b; Huey and Kingsolver 1989). Optimal performance of physical and biochemical processes is achieved at a specific T_b known as the optimal temperature (T_o; after Blouin-Demers et al. 2003) or within a restricted range of preferred temperatures (T_{set} after Hertz et al. 1993; delimited by T_{setmin} and T_{setmax}). Optimal performance can vary for different functions and therefore, different processes can have different distinct T_o (Du et al. 2000; Van Damme et al. 1991; Xu et al. 1999). The critical thermal limits, delimited by CT_{min} and CT_{max} (Huey and Stevenson 1979) are associated with the extreme ends of the tolerance zone.

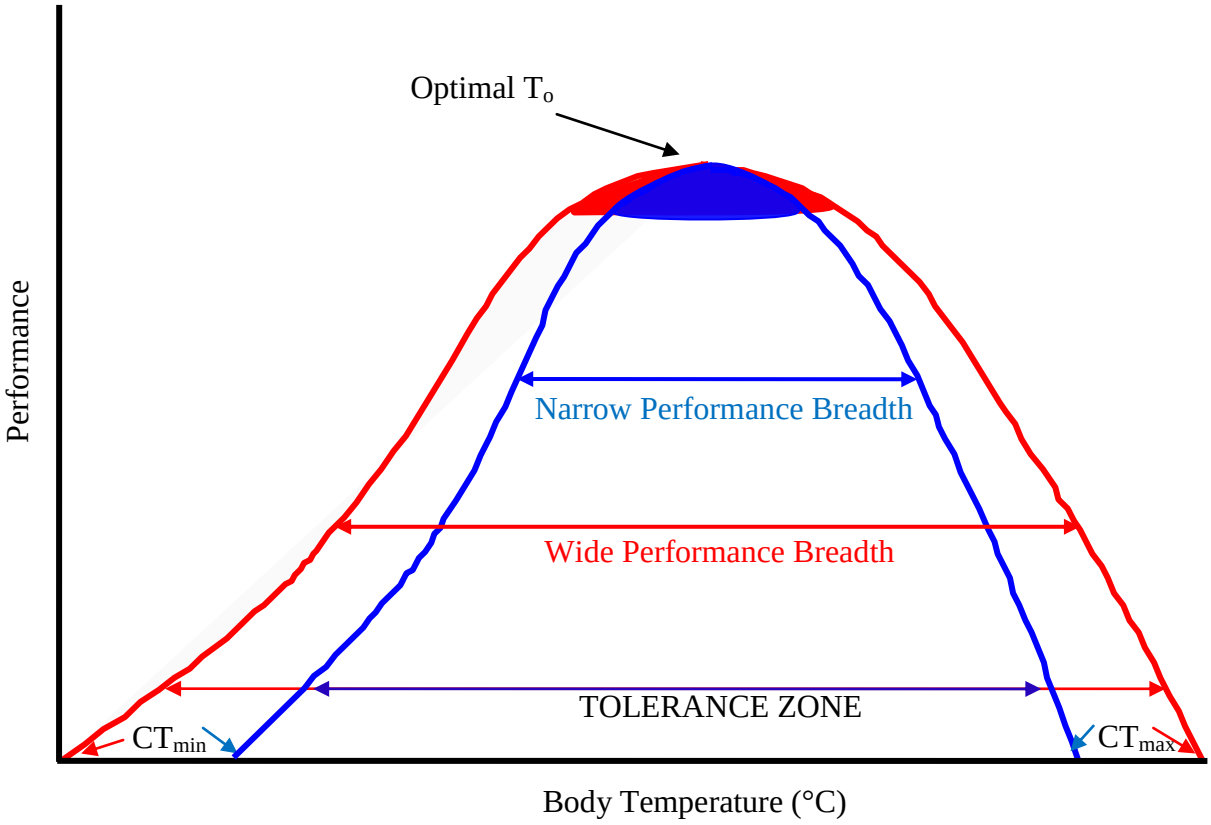

Figure 1.1 Performance curves illustrating the variation between a narrow and wide performance breadth and the optimal performance range on either side of the optimal temperature (T_o) at which performance is maximized. Critical lethal temperatures, delimited by CT_{min} and CT_{max} form the upper and lower boundary limits of the tolerance zone. (Adapted from Huey and Stevenson, 1979; for variation in curve shape see Huey and Kingsolver, 1989).

The performance curve illustrates that the rate of a physiological process increases over a range of T_b up to T_o and then declines beyond that point (Angilletta et al. 2002a; Huey 1982). Optimal temperatures for reptilian biological functions generally vary between 25 and 35°C (Al-Johany and Al-Sadoon 1996; Avery 1982; Bennett 2004; Du et al. 2000). Body temperatures above 35°C can lead to increased stress related to an overload in heat gain and a T_b above 40°C is often lethal (Withers 1992).

Variation in T_o for different performance functions suggests that not all processes are being optimized at the same time (Xiang et al. 1996). For example, in the Grass Lizard, *Takydromus septentrionalis,* T_o for sprint speed was 32°C, whereas T_o for food passage was 36°C (Xiang et al. 1996). Ecologically, this may impart a selective and energetic advantage. Reducing energetic demands for optimization of a specific function and instead selecting a preferred body temperature (T_{sel} or T_{pref}) which allows adequate functioning of multiple processes instead of optimal functioning of a single process can occur (Du et al. 2000; Huey 1982). Theoretically, T_o is selected to maximize fitness over the performance breadth, but in reality many ectotherms do not achieve T_o because most are imperfect thermoregulators and experience a range of T_b resulting in differences in asymmetry of performance breadths (Martin and Huey 2008).

Performance breadths vary intra- and interspecifically for the same physiological process (Angilletta et al. 2002a), which affects species adaptability to thermal changes in the environment, their distribution and overall success (Glanville and Seebacher 2006). Selection of thermal environments that are relatively stable result in an individual experiencing less variation in T_b (Huey 1991) and a narrower performance breadth (Gilchrist 1995). Conversely, heterogeneous environments can cause large fluctuations in T_b, increased phenotypic flexibility and a wider performance breadth (Kassen 2002). In closely related species with overlapping distributions, the species with a larger distribution experiencing greater environmental heterogeneity should develop a wider performance breadth as a more successful strategy (Huey and Hertz 1984).

A thermally constant environment should favour a species capable of achieving specific T_o more often within a narrow temperature range (Blouin-Demers and Nadeau 2005). This trade-off between performance breadth and T_o in reptiles, referred to as the 'jack-of-all-temperatures is a master of none' hypothesis (Huey and Hertz 1984), is also viewed as a plausible explanation for the selection of a specialist versus generalist strategy. If costs associated with flexible responses to environmental conditions outweigh benefits

selective pressures would increase towards specialization (Gilchrist 1995; Huey and Slatkin 1976). Therefore, measuring performance across a range of temperatures for individuals and populations is important not only to determine the adaptive capacity to temperature changes but to assess the degree of flexibility within a trait that may have long term implications to the survival of a species.

The adaptive capacity known as phenotypic flexibility is defined as changes in an individual's phenotype related to the degree of plasticity in the expression of the genotype. It is considered an adaptive response to rapid increases in environmental heterogeneity (Seebacher 2005). The ability to adjust to increasing environmental stochasticity and then quickly reverse the adjustment may impart a selective advantage (Piersma and Drent 2003). In contrast, populations with limited behavioural, physiological or morphological trait flexibility would have a minimal response to rapid environmental shifts (Bacigalupe et al. 2004). Thus in homogeneous environments, selective pressures on trait flexibility decrease if costs associated with increased flexibility are greater than the advantages (Sinclair et al. 2006).

Studies of the impact of phenotypic flexibility have recently focused on metabolism, defined as the energy expended at a cellular level for the biochemical synthesis, transportation and assimilation of nutrients (Braefield and Llewellyn 1982). Metabolic rate (MR), the energy used per unit of time and for the breakdown of materials, varies inter- and intraspecifically. Metabolic rate is influenced by changes in T_b which can affect other life-history traits (Angilletta 2001b). In ectotherms, and specifically snakes, sensitivity to changes in temperature is more pronounced than in endotherms because they rely predominantly on external sources for heating and cooling (Withers 1992). Studies show that in reptiles, in particular, temperature shifts significantly affect MR (Dorcas et al. 2004; Zaidan and Beaupre 2003) and digestion (Secor 2009).

1.2 Metabolism

Metabolism and associated components, including digestive assimilation and efficiency, are measured in three ways (Schmidt-Nielsen 1997):

1. The difference between total energy intake and energy excreted in faecal matter and urine.
2. The determination of total heat production of the animal.

3. The volume of oxygen consumed in oxidative processes.

Various endogenous and exogenous factors can affect a reptile's MR including, T_b (Al-Johany and Al-Sadoon 1996), ecdysis (Thompson and Withers 1999), digestion (Secor and Faulkner 2002), reproductive state (Finkler 2006), season (Southwood et al. 2006), time of day (Roe et al. 2004), age (McCue and Lillywhite 2002), gender (Beaupre and Zaidan 2001) and M_b (Dorcas et al. 2004). In addition, the size, type and content of a meal also influence MR during digestion (Bontrager et al. 2006; Janes and Chappell 1995; Secor et al. 2007; Toledo et al. 2003). Larger prey items and intact prey that contain bones, feathers or fur have been shown to increase MR relative to digestion of liquid or small meals (Boback et al. 2007; Secor 2003). Metabolic rate increases when T_b increases and is influenced by the process of ecdysis, digestion and reproductive state. Season affects MR indirectly. Factors associated with changes in season, including temperature shifts, resource availability and activity levels influence total energy available, energy consumed and energy used (Andrade et al. 2004; Bennett and Dawson 1976). The two most influential and widely studied factors that affect MR are M_b and T_b.

Much of the variation in MR is attributable to M_b. Metabolic rate scales allometrically to M_b illustrated by the equation $MR = aM^b$, where 'a' is the mass coefficient, 'M' is mass and 'b' is the mass exponent (Withers 1992). If 'b' = 1, then MR would be directly proportional to M_b, but if 'b' varies from one then MR is not directly proportional to M_b and the relationship is not linear. The relationship between M_b and MR is most often curvilinear (Withers 1992). As M_b increases, whole animal MR increases (Bennett and Dawson 1976; Roe et al. 2005) but not at the same rate, an indication of why 'b' is not usually equal to one. To factor out the effect of M_b on MR, mass-specific MR is used for intra- and interspecific comparisons. The effect of M_b can be accounted for by making the relationship linear using the equation $(\log_{10} MR) = (\log_{10} a) + b(\log_{10} Mass)$. Variation in MR can then be analyzed intra and interspecifically.

The existence of a universal value for the mass exponent continues to be debated (Gillooly et al. 2001; Kleiber 1975; White et al. 2006). Use of a standardized mass exponent of 0.75 or 0.67 is no longer broadly accepted for most reptiles, mammals or birds as it is highly variable between species (Andrews and Pough 1985; McNab 2008; White et al. 2007). For reptiles, the mass exponent varies considerably between 0.50 and over 1.0 (for example see Andrews and Pough 1985; Maxwell et al. 2003; Secor and Boehm 2006; Thompson and Withers 1992); suggesting that the relationship between and within reptilian groups is not linear, and MR is not directly proportional to M_b.

Variation in MR is also affected by digestive state and activity level. Standard metabolic rate (SMR) is the baseline measurement of metabolic rate in a postabsorptive resting reptile in the inactive phase of their daily activity cycle at a specified temperature (Withers 1992). The increase above SMR related to digestion in an absorptive reptile is known as specific dynamic action (SDA; Coulson and Hernandez 1979; Jobling and Davies 1980; Secor 2009).

1.2.1. Standard Metabolic Rate and Resting Metabolic Rate

In reptiles, the minimum energetic requirement to sustain vital physiological functions or the maintenance cost of survival is SMR (Bedford and Christian 2001; Bennett and Dawson 1976). Standard MR can be measured by the volume of oxygen (VO_2) consumed, carbon dioxide produced or both using indirect calorimetry on a fasted, resting (unstressed) animal in the dark during the inactive phase of their diel cycle (Bennett and Dawson 1976; McDonald 1976; Withers 1992; Zaidan 2003). The conditions under which SMR is measured and the statistical determination of SMR vary between studies, but is most frequently measured as an average of the lowest 25% or 50% of all metabolic measurements over a certain period of time or as the lowest measure of MR for a consistent period within the sampling time (i.e., the lowest MR that is consistent for one hour; Hopkins et al. 2004; Roe et al. 2004).

Measurements of SMR may underestimate maintenance costs that free-ranging ectotherms incur because it ignores ecologically important conditions normally experienced by ectotherms in the field, including digestive state (i.e., whether the animal is absorptive or post-absorptive), time of day, season and reproductive state (Niewiarowski and Waldschmidt 1992). In the field, movement due to predator avoidance or T_b regulation (for example see Al-Johany and Al-Sadoon 1996; Birchard et al. 2006; Finkler 2006; Penick et al. 2002) and fasting duration can affect SMR increasing maintenance costs (Bennett and Dawson 1976). Prolonged periods of fasting and inactivity can significantly depress SMR measurements (Withers 1993). Bedford and Christian (2001) found that fasting for 56 and 45 days in adult and hatchling Water Pythons, *Liasis fuscus*, respectively, significantly lowered SMR compared to that of postabsorptive but not fasted *L. fuscus*. Niewiarowski and Waldschmidt (1992) suggest that SMR may not be an ecologically relevant measurement of maintenance MR because it underestimates MR as

most animals in the wild will have food in their stomachs and variable rates of O_2 consumption during inactive periods.

Resting metabolic rate (RMR) is sometimes used in lieu of SMR (Bennett and Dawson 1976). By definition, RMR is less restrictive in terms of testing because the animal can be measured at any time under illuminated conditions in a fasted, resting state (Zaidan 2003), or resting in a thermoneutral state, but that is not necessarily postabsorptive (Blatteis et al. 2003). Nevertheless, a large number of studies use SMR as a benchmark for comparing inter- and intraspecific MR and minimum maintenance costs (Christian et al. 1999; Hopkins et al. 2004; Secor and Diamond 2000; White et al. 2006; Zaidan 2003).

Standard MR describes the minimum energy required to maintain vital life functions, but additional energy must be acquired through feeding to perform other physiological processes and to build energy reserves during periods of food scarcity. While feeding and digestion add valuable energy and nutrients to the total sum available, the process to complete digestion uses a proportion of the energy consumed. During feeding, energy demands increase leading to an increase in oxygen uptake rates which is referred to as specific dynamic action. To determine the amount of energy allocated directly to feeding and digestion, leaving the remaining energy for other processes, it is necessary to measure the total energy consumed and used during digestion and assimilation of nutrients.

1.2.2. Specific Dynamic Action

One of the most frequently studied effects on ectotherm metabolism is feeding and digestion because cellular metabolism provides the energy required for most other physical and physiological functions. The feeding process and digestion of prey items may cause an increase in MR and T_b through behavioural thermoregulation (Greenwald and Kanter 1979) or endogenous heat production (e.g., *Python molurus*; Marcellini and Peters 1982 and *Crotalus durissus*; Tattersall et al. 2004). Elevation of MR and the associated increases in energetic expenditure above SMR after feeding is termed specific dynamic action (SDA; see McCue 2006; and Secor 2009 for historical derivation of SDA). Specific dynamic action is the total energetic cost associated with the breakdown and digestion of food and nutrient assimilation including transportation and absorption (Beaupre 2005; Kleiber 1975; Secor 2009).

Specific dynamic action can be calculated similarly to SMR based on VO_2 consumed or CO_2 produced, but is usually converted to an energetic equivalent in kJ (Gessaman and Nagy 1988). To convert SDA measurements of VO_2 to energy equivalents (kJ), a respiratory quotient (RQ, VCO_2/VO_2; Withers 1992) for uricotelic animals of between 0.70 and 0.80, and an energy equivalent of 18.4 kJ/g protein or 19.8 kJ/L O_2 can be assumed resulting in a small error of 1.5% for typical carnivores that digest a meal composition of 80:15:5 (protein: fat: carbohydrates; Gessaman and Nagy 1988). Many studies also quantify the time to peak MR following feeding, the peak MR, the duration of elevated metabolism, and/or the factorial scope (Peak MR/ SMR or RMR; Robert and Thompson 2000; Secor et al. 2007).

Measurements of MR, factorial scope, digestive efficiency and duration are influenced by multiple factors and are highly variable within and between species. Changes in T_b (Wang et al. 2003), ecdysis (Thompson and Withers 1999), age (Slip and Shine 1988a), M_b (Secor and Faulkner 2002), meal size (Roe et al. 2004) and meal type (Pan et al. 2005a, 2005b) can significantly affect the SDA response. Greater protein content in a meal and larger meals also influence the duration of SDA and peak VO_2 (Coulson and Hernandez 1979; Robert and Thompson 2000). Factorial scope can be up to 17 times greater than SMR in *P. molurus* (Secor and Diamond 1995) and 18.5 times greater for *Boa constrictor* (Secor and Diamond 2000), but less than two for species of Testudines (Pan et al. 2005a), Squamates (Robert and Thompson 2000) and Crocodylians (Starck et al. 2007). In addition, the increased MR often coincides with an increase in T_b to optimize digestive functioning known as postprandial thermophily (Bontrager et al. 2006; Sievert and Andreadis 1999; Tattersall et al. 2004).

As T_b increases, the SDA response and the scope increase, while the duration of elevated metabolism is reduced resulting in a shorter digestion period (Greenwald and Kanter 1979; Secor et al. 2007). In reptilian feeding studies, the majority of species tested completed digestion within 10 - 14 days, when temperatures ranged between 25 - 35°C (Andrade et al. 1997; Bedford and Christian 2001; Groβmann and Starck 2006). At temperatures below 25°C, the duration of digestion is longer for many species (Sievert et al. 2005), but digestive efficiency and assimilation are relatively independent of temperature (Greenwald and Kanter 1979; McConnachie and Alexander 2004; Wang et al. 2003). Skoczylas (1970) found that digestion in the Grass snake, *Natrix natrix* was significantly slowed or completely hindered at temperatures of 15°C and 5°C, respectively, resulting in regurgitation of the meal. In the Flat lizard, *Platysaurus intermedius wilhelmi*

feeding ceased below 12°C (Alexander et al. 2001). There are exceptions, however, and some species fail to show postprandial thermophily (Tu and Hutchison 1995) or significant variation in SDA between different meal types (Grayson et al. 2005).

In environments characterized by highly erratic or seasonally fluctuating food sources, reptiles exhibit adaptive biochemical and physiological responses to food deprivation (Wang et al. 2006), including gut atrophy and the down-regulation of organs that are energetically expensive to maintain (Holmberg et al. 2002). After feeding, increases in MR coincide with the expansion or thickening of internal organs including the liver, epithelial mucosa and the small intestine (Bramwell 2006; Groβmann and Starck 2006; Starck and Beese 2002). Upon ingestion of a meal, significant SDA responses relative to SMR levels were recorded in intermittent feeders and extreme sit-and-wait foragers, including *P. molurus*, and the Timber Rattlesnake, *Crotalus horridus*. Large SDA responses may occur because of the significant energy expenditure required in the physiological upregulation of the gut after long periods of food deprivation (Secor and Diamond 1995; Zaidan and Beaupre 2003).

Further studies on the physiological effects of feeding and fasting in reptiles will aid in understanding:

1. The intra- and interspecific variation of pre- and postprandial metabolic responses.
2. The effect of temperature on digestive efficiency, digestive rate and cellular modifications in reptiles that have different foraging modes.
3. The evolutionary and adaptive implications that the cost of digestion has on distribution.
4. The physiological implications that dietary specialization may have on energetic costs and savings in trophic specialists.

Increased dietary specialization may lead to more efficient prey handling and digestion for preferred prey relative to dietary generalists in terms of time and energy expended (Britt and Bennett 2008). Since extinction risk and prey depletion increases with increased specialization, selective pressures would dictate that, for the preferred prey item, prey handling and digestion would need to be more time and energy efficient to be advantageous (Berumen and Pratchett 2008; Mori and Vincent 2008). In general, specialization evolves when there is increased efficient use of a resource or if interspecific competition is increased (Futuyma and Moreno 1988).

1.3 Dietary Specialization

Selective pressures towards specialization often do not follow an outwardly visible pattern, but it is generally assumed that specialization is associated with a set of observable trade-offs in fitness and performance (Futuyma and Moreno 1988), a narrower niche breadth, resource abundance and density dependence (i.e., the number of other individuals undertaking the same strategy; Wilson and Yoshimura 1994). Phenotypic, habitat and behavioural specialization can lead to greater efficiency in prey acquisition and energy assimilation (Britt and Bennett 2008; Cruz-Neto et al. 2001; Mori and Vincent 2008), predator avoidance (Kumagai 2008) and general physiological processes such as thermoregulation (Gilchrist 1995). Recent studies have shown that increased intraspecific variation as a result of population increases and greater intrapopulation competition may be an important influencing factor for behavioural and physiological divergence and specialization, which over evolutionary time periods could lead to speciation (Bolnick et al. 2003; Tinker et al. 2008).

Increased specialization in habitat or dietary preference can also be an effective strategy in non-seasonal environments characterized by low levels of stochasticity and fluctuations in resource availability (Wilson and Yoshimura 1994). Competition theory suggests that in stable environments, the risk increases for niche overlap between species due to increased species richness and carrying capacity saturation resulting in increased competition and the probability of competitive exclusion (Begon et al. 1996). In this context, increased intraspecific competition for space and prey could generate a selective advantage for increased specialization as discovered in *Anolis* lizards in the Bahamas (Losos et al. 1994).

The extent of specialization within a population can be variable and is influenced by an individual's preferences (Spencer et al. 1998). Populations that have a wide niche breadth in terms of dietary requirements and prey selection are considered trophic generalists. Yet, within the population there are individuals that may utilize only one or a small subset of the total available prey items, effectively making them trophic specialists (Fox and Morrow 1981). True dietary specialists in which the population as a whole feeds on few prey types, even when suitable alternatives are available, have a narrower resource base than generalists (Holbrook and Schmitt 1992). A narrow trophic niche constrains

adaptability and increases vulnerability to climatic changes that alter food availability (Berumen and Pratchett 2008; Smith and Remington 1996).

Williams et al. (2008) suggest that heritable variation that limits distribution reduces the adaptive capacity of a specialized species during rapid climatic shifts independent of population size. Extreme dietary specialization is, therefore, considered to be a dangerous strategy contradictory to an evolutionary stable strategy because of the risks associated with prey availability and habitat changes (Smith and Remington 1996). Although specialists may have a higher tolerance for lower prey densities, they can have longer patch residence times than generalist species making them more vulnerable to habitat degradation and extinction (Sloggett et al. 2008).

Although feeding is an important factor particularly in the radiation and evolution of snakes (Gans 1961; Greene 1983), dietary specialization in snakes is considered rare because natural selection has favoured generalists capable of adapting to adverse conditions (Smith and Remington 1996). Most snakes are carnivorous dietary generalists that actively search for prey or are opportunistic sit-and-wait foragers. Morphologically, they have evolved unique adaptations for ingesting prey several times greater than the diameter of their head allowing for capture of multiple prey types (Cundall 1987). Prey usually consists of mammals, birds, reptiles, amphibians and fish, but many species also include eggs in their diets (Orians and Janzen 1974). Very few species of snake feed solely on eggs (see Coleman et al. 1993; Gardner and Mendelson 2003). Thus, snakes in the genus *Dasypeltis* are among a select group in their dietary requirements and morphology. *Dasypeltis* is one of only two genera which are known obligate feeders of whole, freshly laid bird eggs (de Queiroz and Rodríguez-Robles 2006; Groβmann and Starck 2006; Isemonger 1962). *Elachistodon westermanii*, found in parts of Nepal, India and Bangladesh, is the only other snake with known similarities in feeding mechanism and dietary preference of freshly laid bird eggs (Gartner and Greene 2008).

The question then arises of how two species of the same genus with very similar dietary requirements, ecological, behavioural and morphological traits successfully co-exist in overlapping distributions? Brown (1984) suggests that closely related species with a relatively recent common ancestor differ significantly in very few or even one niche dimension due to evolutionary constraints on morphology, physiology or behaviour. Competition theory, however, predicts that competitors for the same resource should show morphological, behavioural, ecological or physiological differentiation as a result of niche differentiation if they are to coexist (Begon et al. 1996). In order for co-existence over an

evolutionary and ecological time-scale, Tinker et al. (2008) propose that a high degree in similarity and overlap of preferences (dietary, spatial or ecological), behaviour and distribution is the result of an abundance of available prey or a food-rich environment. If this is the case, *Dasypeltis* species that have a high degree of similarity in preferences and dietary requirements may be able to coexist because of increased prey availability. While prey abundance can enable the coexistence of species with similar preferences, variation in physiological tolerance limits may play a part in distribution differences and range limitations between similar species (Futuyma and Moreno 1988).

Furthermore, dietary specialization would predictably lead to increased efficiencies in food handling and digestion leading to energy savings. Relative to other snake species with different feeding behaviours (frequent *vs* intermittent feeders) and food preferences (egg meal v*s* rodent meal), dietary specialists, *Dasypeltis inornata* and *D. scabra* should exhibit lower metabolic postprandial responses owing to the liquid content of their meal (Boback et al. 2007) and increased efficiency due to specialization for feeding on a select prey type (Britt and Bennett 2008). Therefore, the metabolic rate of *D. scabra* and *D. inornata*, was estimated and compared to investigate interspecific differences in MR and digestion.

1.4 Aims, Objectives and Predictions

AIMS

The aim of this study was to investigate the effect of temperature, age and body mass on pre- and postprandial metabolic rates in adult and hatchling *D. scabra* and in adults of *D. inornata* to determine if significant variation exists intra- and interspecifically.

OBJECTIVES

A. To determine metabolic rate using closed system respirometry on fasted and fed snakes at five temperatures experienced by snakes in the wild, 20, 25, 27, 30 and 32°C
B. To determine significant inter- and intraspecific differences in MR between species and age groups the following variables were measured as described by Secor and Faulkner (2002):
    1. Body mass (g)

2. SMR (ml O_2 g^{-1} and ml O_2 g^{-1} h^{-1})
3. Peak O_2 (ml O_2 g^{-1} and ml O_2 g^{-1} h^{-1})
4. Scope of peak O_2 (peak O_2/SMR)
5. Duration of postprandial response which is significantly elevated above SMR
6. SDA (kJ and kJ kg^{-1})
7. SDA coefficient (% of the meal's energy content)

PREDICTIONS

As in other species, it is predicted that at higher temperatures the SDA response will be greater relative to SMR, but the duration of elevated MR will be shorter because of the liquid content of the diet. It is also predicted that there will be significant interspecific differences and intraspecific ontogenetic differences between adults and neonates related to body mass and age effects. It is expected that body mass and age will account for much of the variation in MR for absorptive and postabsorptive snakes. Furthermore, it is predicted that mass-specific SMR will be lower in neonates than adults as an energy conservation measure, and may be linked to the rarity of very small bird eggs (≤ 5 mm in diameter) in South Africa. Finally, I predict that SDA will also be lower in neonates in order to allocate more energy for rapid growth rather than the digestive process.

1.5 Study Animal

1.5.1. General Taxonomy

Dasypeltis is a highly specialized genus within the Colubridae (Marais 2004). Presently, eight species, all endemic to Africa, have been identified. *Dasypeltis* is considered a monophyletic genus (Gravlund 2001) with recent taxonomic studies based on mitochondrial DNA sequencing suggesting that the closest extant sister taxon is the genus *Boiga* (Kelly et al. 2003; Lawson et al. 2005). Although morphological differences exist within the *D. scabra* population of South Africa, recent DNA evidence suggests that only the population found in the Northern Cape of South Africa may be a different species. Mitochondrial DNA evidence indicates that the remaining populations across South Africa, however morphologically different, are not distinct species (Bates et al. 2009).

1.5.2. General Biology

Dasypeltis species have evolved a highly specialized feeding mechanism for consuming bird eggs (Rabb and Snedigar 1960). Having significantly reduced dentition and exceptionally pliable skin covering the bottom jaw, whole freshly laid eggs are swallowed. The shell is then punctured by modified vertebral hypapophyses projecting anteroventrally from the oesophagus, the liquid contents swallowed and the shell regurgitated in a compacted boat-like shape (Gartner and Greene 2008). The size of the egg ingested relative to body size and jaw length is significantly larger than an egg consumed by facultative oophagous snakes such as *Elaphe obsoleta* (Rabb and Snedigar 1960) and *Lampropeltis getula* (Gartner and Greene 2008). A 52.0 g *D. scabra* with a head diameter of 10 mm was reported to have consumed a 70.4 g duck egg measuring 46mm in diameter at its widest point (Krupa 1985)

Dasypeltis species lack defence and predation mechanisms commonly found in other species including venom, constrictive ability and teeth (Gans 1961), but have evolved a form of Batesian mimicry of Viperid species with overlapping distributions (Branch 1998; Gans and Richmond 1957). The main models for mimicry include species from the genera *Echis*, *Bitis* and *Causus* (Gans 1961). Mimicry may be the result of increased exposure to predators. Due to their foraging behaviour of actively seeking out the eggs of ground and arboreal nesting bird eggs, they are frequently exposed to potential predators (Gans and Richmond 1957). In South Africa, a *D. scabra* was found dead, hanging from a Common Fiscal Shrike, *Lanius collaris*, nest with three recently ingested egg yolks in its stomach (Bruderer 1991). *Dasypeltis* have also been known to rob nests of birds that are several orders of magnitude heavier than they are. On Schaapen and Meeuw islands off the Western Cape coast of South Africa, regurgitated egg-shells from Cape Cormorant, *Phalacrocorax capensis*, Kelp Gull, *Larus dominicanus*, and Rock Pigeon, *Columba livia*, nests were found. The regurgitated shells were boat-shaped which is characteristic of an egg regurgitated by *Dasypeltis* species (Dyer 1996).

1.5.3 Study Species

For this study, the MR for two species from the genus *Dasypeltis* was investigated. *Dasypeltis scabra* (Common or Rhombic Egg-eater; n = 22) and *D. inornata* (Southern

Brown Egg-eater; n = 4; Figure 1.2) share many behavioural, ecological and morphological qualities. They are predominantly nocturnal, but there have been reports of *D. scabra* feeding during the day (Harvey pers. comm.[1]). *Daspeltis* species are often found in old, unused termitaria (Alexander pers. comm.[2]) and may rely on them for refuge and brumation. Behavioural mimicry of local Viperids is evident in both species, but colouration mimicry appears to exist only for *D. scabra* which mimics the behaviour and coloration of the Rhombic Night Adder, *Causus rhombeatus*, (Marais 2004). Morphologically, both species have small heads with minimal tapering between the head and body, large eyes and a vertical pupil (Branch 1998). Highly agile, *D. inornata* and *D. scabra* have excellent climbing abilities allowing them to feed on the eggs of ground-nesting and arboreal avian species. The species are similar in body size reaching average lengths up to 75cm, although *D. inornata* can grow to over 1m in length (Marais 2004).

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a.

b.

Figure 1.2 a.) *Dasypeltis inornata*, Southern Brown Egg-eater b.) *Dasypeltis scabra*, Common/ Rhombic Egg-eater

The seasonality of available avian eggs for consumption by *Dasypeltis* species is debatable. Groβmann and Starck (2006) indicated that these snakes were restricted to a distinctly seasonal food source based on the avian breeding season characterized by short periods of prey abundance and long periods of fasting in between. Bramwell suggested

that the avian breeding season in the Transvaal region of South Africa was less seasonal than originally thought. No evidence is provided, however, to suggest that these snakes are capable of digesting during cold winter temperatures, nor that the available eggs are chosen by *Dasypeltis* species. The study indicated that only two snakes examined were caught in the winter and makes no mention of egg being found in the gut of these two snakes, but does mention that the only food item found in the gut of 30% of the snakes was egg (Bramwell 2006).

Increases in the size and function of the gastrointestinal tract, normally associated with ambush foragers that experience long periods of fasting, suggests that *D. scabra* may also experience periods of fasting between meals (Groβmann and Starck 2006). The increase in size of the intestine, liver and heart was similar to other snake species that rely on digestive down-regulation in between meals to conserve energy (Groβmann and Starck 2006). Long fasting intervals are normally associated with large bodied sit-and-wait foragers capable of consuming a meal equivalent to 50% or more of their M_b (Bedford and Christian 2001; Marcellini and Peters 1982; McCue et al. 2005; Secor and Diamond 1995; Shine and Fitzgerald 1996; Tattersall et al. 2004). *Dasypeltis* species are not, however, large-bodied, but rather slender snakes whose meal sizes are normally less than 50% of M_b. During periods of low prey availability, these snakes may require down regulation of internal organs to sustain them.

With scant ecological and behavioural data, much of the necessary hard-line data to substantiate these theories is unavailable. In addition, food preference of both species is relatively unknown apart from the occasional report of nest predation in select avian studies (Table 1.1). Based on the number of avian species breeding year round in South Africa, the actual number of bird species whose eggs are preyed upon by *Dasypeltis* species may be substantially larger than the anecdotal accounts of nest predation described in Table 1.1. As there are currently no ecological studies directly associated with the behaviour or nest predation in the wild for *Dasypeltis*, Table 1.1 simply presents an idea of the size of eggs some of the snakes are selecting and possible egg preference. There are currently no known published records of nest predation for *D. inornata* but it is predicted, based on their capacity for arboreal movement, that there is a strong link to an arboreal lifestyle and a diet containing eggs of tree-nesting birds.

Table 1.1 Reports of nest predation by *Dasypeltis scabra* in South Africa

Species	Location/ Province	General Egg-Laying Season	Peak Egg-Laying*	Mean Egg Size (mm)*	Study
Common Fiscal Shrike (*Lanius collaris*)	Limpopo	Oct. - Mar.	Aug. - Dec.	23.5 x 17.7	(Bruderer 1991)
Cape Cormorant (*Phalacrocorax capensis*)	Schaapen Island (Western Cape)	year-round	Sept. - Feb.	54.6 x 35.5	(Dyer 1996)
Kelp Gull (*Larus dominicanus*)	Meeuw Island (Western Cape)	late Sept. - Jan.	Oct.	72.0 x 48.6	(Dyer 1996)
Rock Pigeons (*Columba livia*)	Schaapen and Meeuw Islands (Western Cape)	year- round	n/a	39.0 x 29.0	(Dyer 1996)
Red-Collared Widowbirds (*Euplectes ardens*)	KwaZulu-Natal	Oct. - Mar.	Nov. - Feb.	18.9 x 13.6	(Pryke and Lawes 2004)
Namaqua Sandgrouse (*Pterocles namaqua*)	Northern Cape	Aug - Jan.	Aug. - Jan.	36.1 x 25.2	(Lloyd 2004)
Karoo Prinia (*Prinia maculosa*)	Western Cape	July - Jan.	Aug. - Nov.	16.4 x 11.7	(Nalwanga et al. 2004)
Cape Bulbul (*Pycnonotus capensis*)	Eastern Cape	Sept. - Mar.	Oct. - Nov.	23.6 x 17.1	(Krüger 2004)

*Egg size and laying information adapted from Roberts Birds of Southern Africa VII edition (Hockey et al. 2005)

1.5.4. Distribution and Ecology

Dasypeltis species are found in various habitat types including savannah, montane forest, rain forest, semi-arid desert and coastal regions at both high and low altitudes (Gans 1960; Marais 2004; Trape and Mane 2006). *Dasypeltis scabra* has a larger distribution than *D. inornata*, and within South Africa their ranges overlap considerably. The overall distribution of *D. scabra* extends from the southern Cape region in South Africa into the horn of Africa and includes biomes ranging from open forest and savannah to arid regions, and is excluded only from true desert and closed-canopy forest areas (Branch 1998). *Dasypeltis scabra* has scattered populations throughout most of South Africa, but is heavily concentrated in the northern, north-eastern and south-western regions. The newly separated species, *D. scabra loveridgei*, once part of the *D. scabra* complex, extends from central Namibia south into Calvinia and Williston in the Northern Cape (Bates et al. 2009). *Dasypeltis inornata* has a more limited range and is endemic to the eastern parts of South Africa including KwaZulu-Natal, the Eastern Cape and Mpumalanga and western Swaziland (Figure 1.3). A disjunct population also occurs in the northern part of Limpopo province. It is most commonly found in open coastal woodland and moist savannah (Marais 2004).

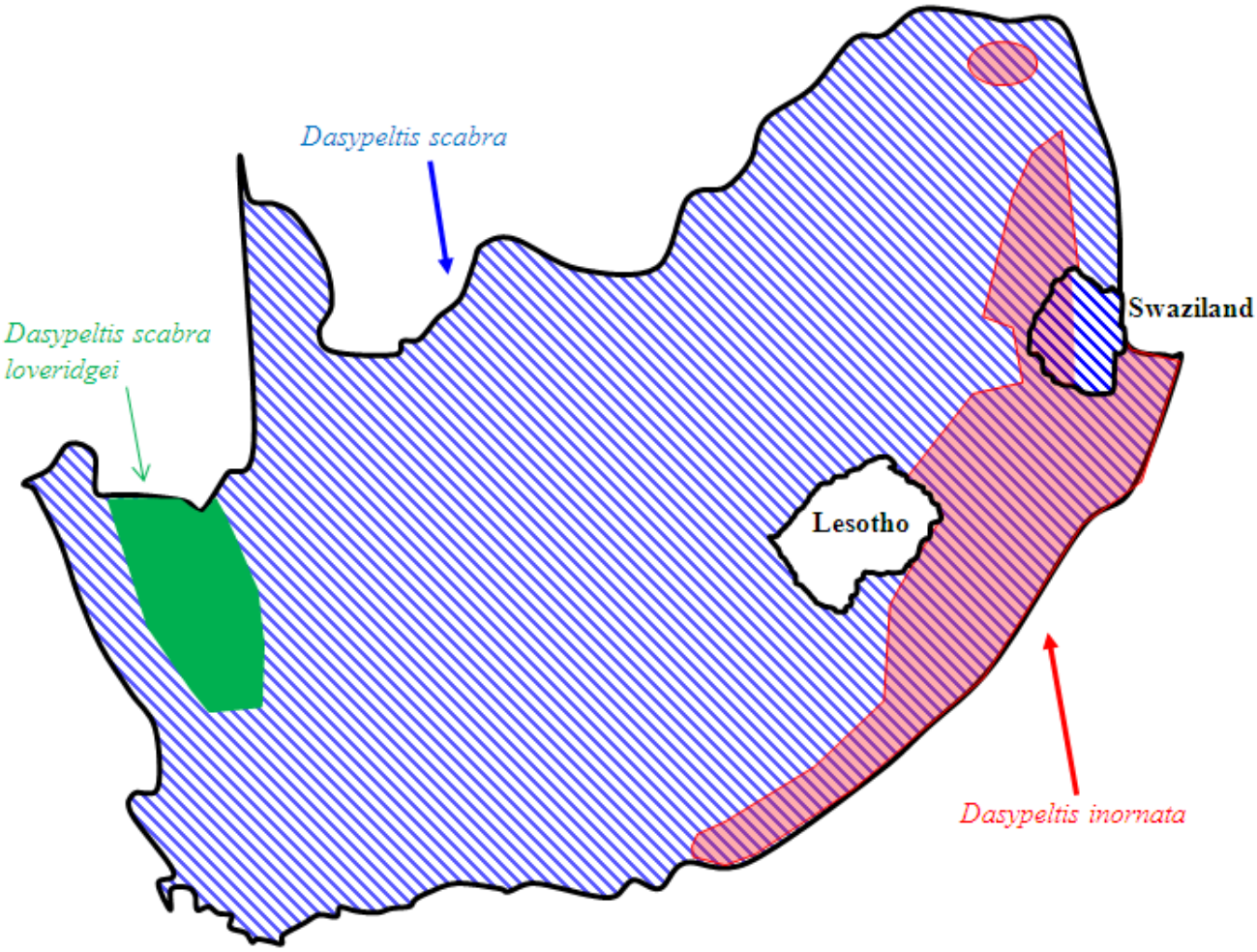

Figure 1.3 Distribution of *Dasypeltis scabra* and *D. inornata* in South Africa and Swaziland adapted from the Avian Demography unit online virtual museum species distribution maps (Southern African Reptile Conservation Atlas 2009 http://vmus.adu.org.za/vm_sp_summary.php). Included is the recently discovered distinct lineage of *D. scabra loveridgei* (Bates et al. 2009).

Populations of *D. scabra* are found throughout South Africa across a wide rainfall gradient. Mean annual precipitation (MAP) ranges from less than 100 mm in parts of *D. scabra*'s range to more than 1200 mm of rainfall annually. *Dasypeltis inornata* appears to be restricted to areas with higher annual rainfall (MAP ≥ 600 mm) along the eastern part of South Africa (Figure 1.4; Schulze et al. 2008). Much of the rainfall in this area occurs during the summer months and peak avian breeding/hatching season (Schulze et al. 2008). MAP ranged from 400 – 600 mm for the *D. scabra* population sampled in this study and from 800 – 1000 mm for the *D. inornata* sample from KwaZulu-Natal (Table 1.2).

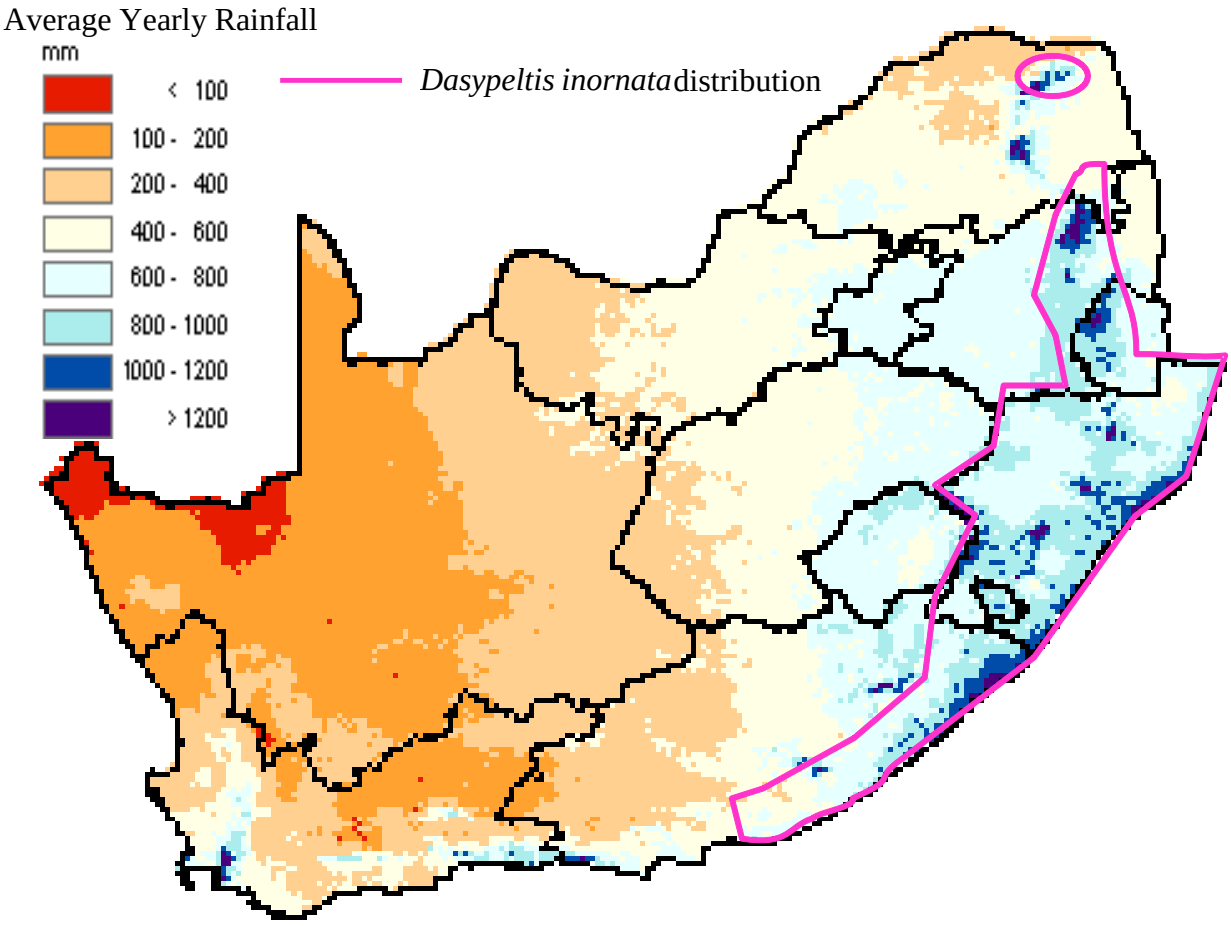

Figure 1.4 Map of average yearly rainfall in South Africa with overlay of *Dasypeltis inornata* distribution. Note that *D. inornata* distribution coincides with areas that receive higher average annual rainfall. Map adapted from Schulze et al. (2008).

In KwaZulu-Natal the avian breeding season extends from spring through early fall, (October – March) and egg-laying peaks from November to February (Table 1.2). Daily temperatures during the peak egg-laying season can range by 15°C from morning to night

time (Table 1.2). Temperature minima and maxima in the Northwest province are generally 2 - 2.5°C higher than the corresponding data from the KwaZulu-Natal province.

Table 1.2 Ecological data for sampled populations of *Dasypeltis scabra* from the Northwest Province and *D. inornata* from KwaZulu-Natal

	Province	
	KwaZulu-Natal	Northwest
Peak avian breeding season	Oct. - Mar.	Sept. - Mar.
Mean annual temperature (°C)	18 – 22	18 – 20
Mean monthly temperature range (°C)	10.0 – 30.0	12.5 – 32.5
Rainfall period	Mid - Late Summer	Mid Summer
Mean annual precipitation (mm)	800 – 1000	400 – 600
Median monthly rainfall range (mm)	60 – 120	40 – 100

Avian information adapted from Hockey et al. 2005. Ecological data Schulze et al. 2008.

Chapter 2 - The effect of temperature, body mass and age on metabolic rate in the Colubrid dietary specialists, *Dasypeltis scabra* and *Dasypeltis inornata*

2.1 Abstract

The additional energy required for digestion and nutrient assimilation – known as specific dynamic action (SDA) - and the duration of gastric breakdown is affected by multiple factors including, body temperature (T_b), meal type and meal size. Liquid meals require less energy to digest than intact prey items consisting of bones and fur. The level of specialization in a species can also affect digestive efficiency as more specialized species would predictably be more efficient feeding on preferred prey types. *Dasypeltis* species are trophic specialists that feed solely on freshly laid bird eggs, digesting only the liquid contents. To examine the effect of specialization, changes in T_b and meal type on the SDA response, we quantified and compared the pre- and postprandial metabolic response of adult and neonate *Dasypeltis scabra* and adult *D. inornata* using closed system respirometry. We measured O_2 consumption rates (VO_2) at five temperatures (20, 25, 27, 30 and 32°C) and found that peak VO_2 increased with temperature, and the peak was reached sooner and then a more rapid decline back to maintenance metabolic rates (SMR) occurred. The SDA response decreased in duration by half when T_b increased from 20 to 32°C. Energy used during digestion (kJ) varied between temperatures but increased as T_b increased for all groups. Increased T_b led to significant increases in metabolic response variables for all snake groups, but there was limited significant intra- and interspecific variation in mass specific MR. Adult *D. inornata* and neonate *D. scabra* tended to have higher pre- and postprandial metabolic rates than adult *D. scabra*. Metabolic scope (2.23 – 3.73) and SDA (0.38 – 13.19kJ) were some of the lowest reported for any snake species across temperature trials. Duration of digestion was, however, 1 – 2 days longer than most species for a meal similar in mass at the same T_b. Specialization and digestion of liquid meals may play a part in reducing the energy demand during feeding, but fail to show added benefit in terms of a decrease in duration of digestion.

2.2 Introduction

Nutrient assimilation supplies the energy necessary for maintenance, activity, growth and reproduction (Congdon et al. 1982). Meal digestion, in turn, requires energy due to the cost of gastric breakdown, transport, assimilation and synthesis of nutrients (Coulson and Hernandez 1979; Secor 2003). Among vertebrates, the postprandial metabolic response is characterized by a rapid increase in metabolic rate (MR), followed by a slower decline to pre-feeding levels, the duration of which is determined by the time it takes to fully digest and assimilate a meal (Secor 2009). The cumulative energy expended above the maintenance metabolism (basal or standard metabolic rate; SMR) related to ingestion, digestion and assimilation of a meal is commonly referred to as specific dynamic action (SDA; reviewed by McCue 2006 and Secor 2009).

Similar to other measures of metabolism (basal, standard, activity), SDA is influenced by body temperature (T_b; Secor et al. 2007), body mass (M_b; Roe et al. 2005) and body composition (reviewed by Secor 2009). In addition, characteristics of the meal, including meal type (Secor and Faulkner 2002), size (Secor and Diamond 1997) and composition (Boback et al. 2007), can have a significant impact on postprandial MR and the SDA response. Feeding frequency can also affect the SDA response. For a given relative meal size and T_b, infrequently feeding snakes experience a larger and longer postprandial metabolic response, and hence a greater SDA than frequently feeding species related to gut up-regulation (Secor and Diamond 2000).

Although a wealth of studies have explored the effects of animal and meal characteristics on SDA in snakes, few have examined differences due to unique feeding habits and dietary specialization (Britt and Bennett 2008; Groβmann and Starck 2006). While many snakes are generalist carnivores that include not only invertebrates and vertebrates in their diet, but eggs as well, some species are trophic specialists feeding solely on squamate eggs (e.g., *Prosymna* spp.; Broadley 1979; *Oligodon formosanus*; Coleman et al. 1993) or bird eggs (*Dasypeltis*; Gartner and Greene 2008). Yet, only two SDA studies are known to have included eggs as a meal choice (Christel et al. 2007; Groβmann and Starck 2006) even though meal type and composition affect the SDA response.

Digesting intact meals comprised of bones, tissue, chitinous carapace or fur is energetically costly (Boback et al. 2007; Secor et al. 2007). Including liquid meals in a

diet would save energy. Less energy is expended to break down a liquid meal relative to an intact meal (Christel et al. 2007). Over an evolutionary timescale, it is possible that a diet that was less energetically expensive to digest may have been advantageous and influenced the selective process in the egg-eating specialization of snakes. In theory, energy savings based on liquid egg consumption should be most apparent in a species that specializes on digesting the liquid contents as specialization often coincides with increased efficiency. Thus, *Dasypeltis* species which are specialized feeders of the liquid contents of freshly laid bird eggs will be used to investigate whether digestive costs are less for a liquid diet.

At 30°C for a chicken egg meal equal to 20% of M_b, *D. scabra* exhibited a lower peak MR and a reduced postprandial metabolic response relative to other snake species consuming a similar sized meal at the same temperature because of the lack of enzymatic breakdown (Groβmann and Starck 2006). Realistically, *Dasypeltis* species encounter a larger range of ecologically relevant ambient temperatures (T_a) at which they could consume eggs based on the extended length of the egg-laying season (Hockey et al. 2005). Therefore, to examine the sensitivity of metabolic rate to T_b changes, the postprandial metabolic response was quantified across a range of ecologically relevant T_b predetermined by environmental conditions and distribution (20 - 32°C; see Schulze et al. 2008 for ecological data). In addition, interspecific, age and M_b effects were also examined using neonate and adult *D. scabra* and adult *D. inornata*. It was predicted that the reduction in the postprandial metabolic response would be similar across all groups and that regardless of age or species or T_b, all *Dasypeltis* groups tested would exhibit reduced peak MR and postprandial responses relative to other species. Finally, it was predicted that increases in T_b would result in higher peak MR and a more rapid return to baseline MR.

2.3 Materials and Methods

2.3.1 Animals and Their Maintenance

Dasypeltis scabra is a widespread egg-specialist found throughout much of the southern and eastern parts of Africa, while *D. inornata* has a limited distribution, endemic to the eastern parts of South Africa and western Swaziland. For this study, we measured post-feeding metabolic responses and quantified SDA of adult and neonate *D. scabra* and adult

D. inornata. Four *D. inornata* were wild-caught in KwaZulu-Natal, South Africa, and 10 adult *D. scabra* were wild-caught in the Northwest Province, South Africa. Neonate *D. scabra* (n = 12) were hatched from clutches laid in the laboratory by six of the *D. scabra* adults. Neonates were classified as snakes six months or younger. Body mass and snout-vent length (SVL) averaged 68.0 ± 6.1g and 650 ± 80mm, respectively for adult *D. inornata*, 54.5 ± 2.80g and 517 ± 32mm for adult *D. scabra* and 4.78 ± 0.13g and 230 ± 7mm for neonate *D. scabra*.

Snakes were housed in custom-made wooden and glass terraria (60 x 30 x 45cm or 90 x 30 x 60cm) within a temperature-controlled room and maintained on a 12L:12D cycle at 24 ± 2°C. Snakes were fed 2 or 3 eggs once every 3-4 weeks with water available *ad libitum*. Eggs were obtained from local bird breeders and included those of Budgerigar, *Melopsittacus undulatus*, Common Quail, *Coturnix coturnix*, Japanese Quail, *Coturnix japonica* and Bantum Chicken, *Cochin bantum*.

2.3.2 Experimental Procedure and Measurement of Oxygen Consumption

Closed-system respirometry was used to measure oxygen consumption rates (VO_2) of fasted and fed snakes (see Secor and Nagy 1994; Vleck 1987) at T_a of 20, 25, 27, 30 and 32°C. The sequence of trials was randomized, and trials were conducted in the following order 25, 32, 27, 20 and 30°C. Prior to metabolic trials, snakes were fasted for a minimum of three weeks to ensure they were postabsorptive. All metabolic trials were conducted in a constant environment room with a 12L:12D cycle. Before each trial, snakes were weighed and placed individually into plastic opaque air-tight respirometry chambers (430 – 2600ml) and allowed to acclimate to the chambers for a minimum of 48 hours. Respirometry chambers were fitted with incurrent and excurrent air ports, each attached to a 3-way stop cock. Silicon tubing (5 mm θ) attached to the stop cocks and air pump via gang valves allowed air to pass freely through the chamber.

For all metabolic measurements, an initial 50ml air sample was withdrawn from the excurrent air port and then both the incurrent and excurrent air ports were closed. One hour later, the excurrent port was opened and a second 50ml sample was withdrawn. After withdrawing the second air sample, both air ports were reopened and room air was pumped continuously through each chamber. The 50ml air samples were pumped (100ml min^{-1}; New Era Pump NE-510, Wantagh, New York, USA) through a column of water absorbent (Drierite; W.A. Hammond Drierite Co., Xenia, OH, USA) and CO_2 absorbent (soda lime)

into an O_2 analyzer (Ametek S-3A/1, AEI Technologies, Pittsburgh, Pennsylvania, USA). Whole-animal (ml O_2 h^{-1}) and mass-specific (ml O_2 g^{-1} h^{-1}) rates of O_2 consumption were calculated and corrected for standard pressure and temperature. Ambient temperature and pressure were measured using a Kestrel 4000 Pocket Weather Tracker (Nielsen-Kellerman, Boothwyn, Pennsylvania, USA).

Each metabolic trial began by measuring fractional oxygen consumption of fasted snakes to determine individual standard metabolic rate (SMR). Measurements of VO_2 for each fasted snake were conducted twice a day at 08h00 and 20h00 for three consecutive days. After the final SMR measurement, snakes were tube-fed a meal of mixed yolk and albumen chicken egg equal to 20% of body mass. Following feeding, snakes were returned to their respirometry chambers and VO_2 was measured twice a day (08h00 and 20h00) for the next five days. Thereafter measurements were taken each morning at 08h00 for 7-12 additional days. Water was provided *ad libitum*.

To calculate SMR and mass-specific SMR (MSMR) the following equations were adapted from Vleck (1987):

Equation 1.

$$SMR\ (ml\ O_2\ h^{-1}) = (V_c - V_s - V_w)*((F_i/100) - (F_e/100))*(P/1000)*t$$

Equation 2.

$$MSMR\ (ml\ O_2\ g^{-1}\ h^{-1}) = [(V_c - V_s - V_w)*((F_i/100) - (F_e/100))*(P/1000)*t] / M_b$$

Where V_c = volume of the chamber

V_s = volume of the snake (1g was assumed to equal 1ml)

V_w = volume of the water and water tray in chamber

F_i = initial fractional concentration of O2

F_e = final fractional concentration of O2

P = pressure standardized to STP

t = time (h)

M_b = body mass (g)

2.3.3 Quantification of SDA and Statistical Analysis

Postprandial and SMR measurements indicated that both *Dasypeltis* species including neonates exhibited a distinct circadian rhythm of night-time activity as VO_2 measured at 20h00 averaged 42.5% greater than at 08h00. The SDA response was therefore quantified

based on O_2 consumption values at 0800h to reduce the effect of elevated metabolic rate not related to digestion and assimilation. For each metabolic trial the following variables were quantified:

1. SMR (lowest VO_2 measured in postabsorptive snake during the inactive phase of the diel cycle),
2. Peak VO_2 (recorded after feeding),
3. Digestive scope of peak VO_2 (peak VO_2/SMR),
4. Duration (post-feeding significant elevation of VO_2 above SMR),
5. SDA (kJ and kJ/kg; total energy expended related to digestion over the duration of significantly elevated VO_2 quantified as the area under the curve of elevated VO_2 levels minus SMR which significantly differed from SMR),
6. SDA coefficient (SDA quantified as a percentage of the energetic content of a meal).

SDA was calculated as the additional O_2 consumed above SMR over the duration of significantly elevated consumption rates and that value multiplied by 19.8 J ml^{-1} O_2 assuming the catabolism of the dry matter was 65% protein, 35% fat and 5% carbohydrate and a respiratory quotient (RQ) of 0.72 (Gessaman and Nagy 1988). The energy content of the meal was calculated by multiplying the meal wet mass by the energy equivalent (kJ g^{-1} wet mass) determined using bomb calorimetry. Chicken egg yolk and albumen were individually freeze dried. Freeze-dried samples (0.5g) were ignited in a bomb calorimeter (isothermal CP500, Digital Data Systems, Randburg, Johannesburg, South Africa) to determine dry mass energy content. Wet mass energy equivalent of the egg excluding the shell (7.59 kJ g^{-1}) was calculated as the product of the individual wet mass energy equivalents for yolk and albumen and the individual masses of the yolk and albumen divided by the average mass of an egg (Davies unpubl.[3]).

A repeated-measures analysis of variance (RMANOVA) was used for each SDA trial to determine significant effects of time (duration) between pre- and post-feeding VO_2 with days as the within subjects effects. Post-hoc Tukey pairwise mean comparisons were employed to determine the duration when post-feeding VO_2 returned to levels not significantly different from SMR indicating that while digestion may not have ceased, the

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energy cost of digestion was not significantly different than maintenance costs. It should be noted that this method of determining SDA duration may result in a bias towards shorter rather than longer SDA duration as a result of the discrepancy between noise to signal ratio (i.e. snakes that exhibit low postprandial metabolic responses relative to SMR). To test for significant effects of temperature and taxon on metabolic variables intraspecifically, general linear model repeated measures analysis of covariance (GLM rmANCOVA, body mass as the covariate) were performed on whole-animal data for SMR, peak VO_2 and SDA (kJ) to account for changes in individuals' body mass across trials. For mass-specific metabolic measurements, general linear models repeated-measures analysis of variance (GLM rmANOVA) were used. Concurrently, post-hoc pairwise means comparisons (Tukey) were used to identify specific significant differences among treatments and taxa. For interspecific and ontogenetic tests between *D. scabra* adults and neonates, ANOVA and ANCOVA (body mass as the covariate) tests were carried out on individual temperatures for whole-animal and mass-specific metabolic measurements. Least squares regression analysis was used to examine the relationship between mass and specific metabolic variables. Body mass, SDA, SMR and peak VO_2 were $\log_{10}$ transformed to normalize distributions and linearize relationships for comparison purposes. Resultant *P* values and *F* values with degrees of freedom from the repeated-measured ANOVA and GLM rmANCOVA are reported, and *P* values of selected significant pairwise mean comparisons are provided. The level of statistical significance was designated as $P < 0.05$ and mean values were reported as means ± 1 SE. Statistical tests were performed using Statistica 9.0 (Statsoft®, Tulsa, Okalahoma USA).

2.4 Results

2.4.1 Body Temperature Effects

In both pre- and postprandial adult and neonate *D. scabra* and *D. inornata*, as T_b increased, VO_2 consumption increased, as well as scope and SDA coefficient. For *D. inornata* and *D. scabra*, whole animal and mass-specific (ml O_2 h^{-1} and ml O_2 h^{-1} g^{-1}) SMR and peak VO_2 were significantly affected by changes in T_b (Table 2.1). Body mass was highly significant as a covariate for *D. inornata* SMR and peak VO_2 (SMR $F_{1,14} = 69.333$, $P < 0.0001$, Peak VO_2 $F_{1,14} = 22.398$, $P = 0.0003$), but was only a significant covariate for peak VO_2 at 20

and 25°C for *D. scabra* adults ($F_{1, 2}$ = 252.203, P = 0.0039, $F_{1, 2}$ = 398.218, P = 0.0025). Non-significant *P*-values for *D. inornata* and *D. scabra* adults M_b indicated that time as a factor across trials did not have a significant effect on gain in M_b for adults.

Neonates exhibited significant differences in mass-specific SMR and whole animal and mass-specific peak VO_2 as T_b increased (Table 2.1). Body mass did not account for a significant amount of the variation in SMR ($0.016 < F_{1, 2} < 4.154$, $0.2058 < P < 0.9207$) or peak VO_2 ($0.0486 < F_{1, 2} < 11.809$, $0.0752 < P < 0.8459$) for *D. scabra* neonates, but was significantly different between the beginning and the end of the temperature trials. Scope, SDA (kJ kg^{-1}) and SDA coefficient were significantly affected by changes in body temperature for *D. scabra* adults and neonates (Table 2.1).

While the factorial scope was not significantly different across temperature trials for *D. inornata* ($F_{4, 12}$ = 1.310, P = 0.3211), mass-specific SDA was significantly affected by T_b changes and the SDA coefficient was borderline significant (Table 2.1) For each species and age group, however, post-hoc tests revealed that while T_b changes had significantly affected metabolic responses, each metabolic variable did not differ significantly among all temperatures but only between specific mean comparisons (Table 2.1). Significant differences occurred most often between 20°C and the other four temperature trials.

An increase in T_b from 20 to 32°C resulted in a greater than 200% and 300% increase in SMR and peak VO_2 respectively for all three groups of snakes. The effect of increased T_b on SDA resulted in a similar trend seen in other metabolic variables and as T_b increased, SDA increased for *D. scabra* adults and neonates and *D. inornata*. In addition, increases in T_b resulted in increases in the proportion of energy required for digestion relative to the total energy consumed for all three taxa. The SDA coefficient more than doubled from 20 to 32°C for all groups. Over the range of T_b tested (20 - 32°C), MR for mass-specific SMR and peak VO_2 increased by a factor (Q_{10}) of 2.69 and 3.41 for *D. inornata*, 2.82 and 3.77 for *D. scabra* adults and 2.77 and 4.06 for *D. scabra* neonates.

Changes in T_b also had an effect on the postprandial metabolic response (SDA response). Post-hoc Tukey tests revealed that as T_b increased, the return to preprandial VO_2 rates from peak VO_2 was more rapid resulting in a shorter duration of significantly elevated VO_2 rates above SMR (Figure 2.1). In general for all groups, an increase in T_b from 20 to 32°C reduced the postprandial metabolic response by half (Figure 2.1). For the same meal size and type at the same temperature, the duration to digest the meal was consistently shorter for *D. inornata* than for *D. scabra*. Neonates digested the meal in a

shorter time period than adults except at the highest and lowest trial temperatures (Table 2.1 and Figure 2.1).

Table 2.1. Body mass, meal size, pre- and postfeeding whole animal and mass-specific metabolic response variables including standard metabolic rate (SMR), peak oxygen consumption, scope of peak, duration, specific dynamic action (SDA) and SDA coefficient for *Dasypeltis inornata* and *D. scabra* adults and neonates in response to five temperature treatments.

	Temperature (°C)						
Variable	20	25	27	30	32	*F*	*P*
Dasypeltis inornata							
no. per trial = n	4	4	4	4	4		
Body Mass (g)	65.20 ± 14.23	61.66 ± 12.74	62.93 ± 12.94	71.33 ± 16.32	65.08 ± 13.59	$F_{4,12}$ = 2.765	0.0770
SMR (ml O_2 h^{-1})	1.03 ± 0.20^{a}	1.70 ± 0.38^{a,b}	2.30 ± 0.45^{b,c}	3.14 ± 0.67^{c}	3.27 ± 0.58^{c}	$F_{4,14}$ = 18.891	< 0.0001
SMR (ml O_2 g^{-1} h^{-1})	0.02 ± 0.0007^{a}	0.03 ± 0.002^{b}	0.04 ± 0.003^{c}	0.04 ± 0.001^{c,d}	0.05 ± 0.003^{d}	$F_{4,12}$ = 62.866	< 0.0001
Peak VO_2 (ml O_2 h^{-1})	2.36 ± 0.48^{a}	4.00 ± 0.52^{a,b}	6.66 ± 1.39^{b,c}	8.81 ± 2.00^{c}	10.15 ± 1.90^{c}	$F_{4,14}$ = 11.754	0.0002
Peak VO_2 (ml O_2 g^{-1} h^{-1})	0.04 ± 0.004^{a}	0.07 ± 0.01^{a,b}	0.11 ± 0.01^{b,c}	0.12 ± 0.005^{c,d}	0.17 ± 0.02^{d}	$F_{4,12}$ = 27.981	< 0.0001
Scope (Peak VO_2/SMR)	2.33 ± 0.24	2.64 ± 0.42	2.90 ± 0.13	2.76 ± 0.10	3.16 ± 0.31	$F_{4,12}$ = 1.3101	0.3211
Duration (days)	13.5	12.5	7.5	6.5	6.5		
SDA (kJ)	6.00 ± 1.59	9.93 ± 1.14	10.84 ± 2.57	13.18 ± 3.03	13.19 ± 3.33	$F_{4,14}$ = 2.026	0.1458
SDA (kJ kg^{-1})	94.75 ± 16.38^{a}	182.10 ± 35.12^{a,b}	184.10 ± 34.68^{a,b}	186.91 ± 17.92^{a,b}	216.37 ± 39.42^{b}	$F_{4,12}$ = 3.564	0.0388
SDA coefficient (%)	6.24 ± 1.08	12.00 ± 2.31	12.13 ± 2.28	12.31 ± 1.18	13.55 ± 2.75	$F_{4,12}$ = 3.093	0.0577
Dasypeltis scabra adults							
no. per trial = n	8	9	10	8	9		
Body Mass (g)	54.23 ± 7.37	47.31 ± 6.52	51.20 ± 6.19	59.08 ± 8.27	54.53 ± 5.69	$F_{4,28}$ = 0.585	0.6758
SMR (ml O_2 h^{-1})	0.70 ± 0.12^{a}	1.48 ± 0.18^{b}	1.69 ± 0.18^{b}	2.37 ± 0.35^{c}	2.40 ± 0.32^{c}	$F_{4,8}$ = 2.454	< 0.0001
SMR (ml O_2 g^{-1} h^{-1})	0.01 ± 0.0009^{a}	0.03 ± 0.003^{b}	0.04 ± 0.003^{b}	0.04 ± 0.003^{b}	0.04 ± 0.004^{b}	$F_{4,24}$ = 10.793	< 0.0001
Peak VO_2 (ml O_2 h^{-1})	1.53 ± 0.25^{a}	3.10 ± 0.34^{b}	4.24 ± 0.38^{c}	5.73 ± 0.74^{d}	7.22 ± 0.53^{d}	$F_{4,8}$ = 4.823	0.0283
Peak VO_2 (ml O_2 g^{-1} h^{-1})	0.03 ± 0.002^{a}	0.07 ± 0.004^{b}	0.09 ± 0.01^{b}	0.10 ± 0.01^{b}	0.14 ± 0.01^{c}	$F_{4,28}$ = 21.307	< 0.0001
Scope (Peak VO_2/SMR)	2.23 ± 0.09^{a}	2.18 ± 0.19^{a}	2.62 ± 0.21^{a,b}	2.47 ± 0.12^{a,b}	3.30 ± 0.32^{b}	$F_{4,28}$ = 4.179	0.0089
Duration (days)	14.5	13.5	10.5	9.5	7.5		
SDA (kJ)	3.89 ± 0.68^{a}	6.18 ± 1.12^{a,c}	6.76 ± 0.96^{a,c}	9.90 ± 1.36^{b}	9.12 ± 0.82^{b,c}	$F_{4,8}$ = 2.772	0.1026
SDA (kJ kg^{-1})	72.29 ± 8.91^{a}	129.70 ± 19.79^{a,b}	137.92 ± 17.06^{a,b}	182.49 ± 25.00^{b}	178.72 ± 21.18^{b}	$F_{4,28}$ = 7.195	0.0004
SDA coefficient (%)	4.76 ± 0.59^{a}	8.54 ± 1.30^{a,b}	9.09 ± 1.12^{a,b}	12.02 ± 1.65^{b}	11.77 ± 1.40^{b}	$F_{4,28}$ = 7.195	0.0004
Dasypeltis scabra neonates							
no. per trial = n	11	8	11	11	8		
Body Mass (g)	4.66 ± 0.27^{a}	3.98 ± 0.20^{b}	4.46 ± 0.27^{a,c}	5.30 ± 0.26^{a,d}	4.45 ± 0.28^{a,b,c}	$F_{4,28}$ = 12.005	0.0001
SMR (ml O_2 h^{-1})	0.07 ± 0.0005^{a}	0.11 ± 0.01^{a,b}	0.14 ± 0.01^{b,c}	0.19 ± 0.01^{c,d}	0.21 ± 0.009^{d}	$F_{4,8}$ = 0.804	0.5552
SMR (ml O_2 g^{-1} h^{-1})	0.01 ± 0.0009^{a}	0.03 ± 0.002^{b}	0.03 ± 0.002^{b}	0.04 ± 0.003^{b}	0.05 ± 0.004^{c}	$F_{4,28}$ = 24.944	< 0.0001
Peak VO_2 (ml O_2 h^{-1})	0.16 ± 0.01^{a}	0.32 ± 0.02^{b}	0.44 ± 0.04^{c}	0.56 ± 0.03^{c}	0.79 ± 0.05^{d}	$F_{4,8}$ = 5.277	0.0222
Peak VO_2 (ml O_2 g^{-1} h^{-1})	0.03 ± 0.001^{a}	0.08 ± 0.003^{b}	0.10 ± 0.008^{b}	0.11 ± 0.006^{b}	0.18 ± 0.02^{c}	$F_{4,24}$ = 33.771	< 0.0001
Scope (Peak VO_2/SMR)	2.39 ± 0.12^{a}	2.94 ± 0.21^{a,b}	3.36 ± 0.28^{a,b}	3.12 ± 0.29^{a,b}	3.73 ± 0.26^{b}	$F_{4,28}$ = 3.364	0.0228
Duration (days)	16.5	12.5	9.5	8.5	7.5		
SDA (kJ)	0.38 ± 0.03^{a}	0.81 ± 0.05^{a,b}	0.64 ± 0.07^{a,b}	1.03 ± 0.08^{b}	1.02 ± 0.06^{b}	$F_{4,8}$ = 0.357	0.8328
SDA (kJ kg^{-1})	81.96 ± 5.83^{a}	206.97 ± 17.29^{b,c}	146.22 ± 12.94^{b}	198.69 ± 17.8^{b,c}	235.33 ± 20.58^{c}	$F_{4,28}$ = 14.662	< 0.0001
SDA coefficient (%)	5.40 ± 0.38^{a}	13.63 ± 1.14^{b,c}	9.63 ± 0.85^{b}	13.09 ± 1.17^{b,c}	15.50 ± 1.36^{c}	$F_{4,28}$ = 14.662	< 0.0001

Note: Variables are defined in the text. Values are presented as mean ± 1 SE. *P* and *F* values result from GLM rmANOVA for body mass, meal size, SMR (ml O_2 g^{-1} h^{-1}), Scope, Peak VO_2 (ml O_2 g^{-1} h^{-1}), SDA (kJ kg^{-1}) and SDA coefficient. The *P* and *F* values from whole animal variables including SMR (ml O_2 h^{-1}), Peak VO_2 (ml O_2 h^{-1}) and SDA (kJ) result from GLM rmANCOVA (body mass as the covariate). Superscript letters that differ denote significant differences ($P < 0.05$) between means among temperature treatments determined from post-hoc pairwise mean comparisons (Tukey tests) for each variable.

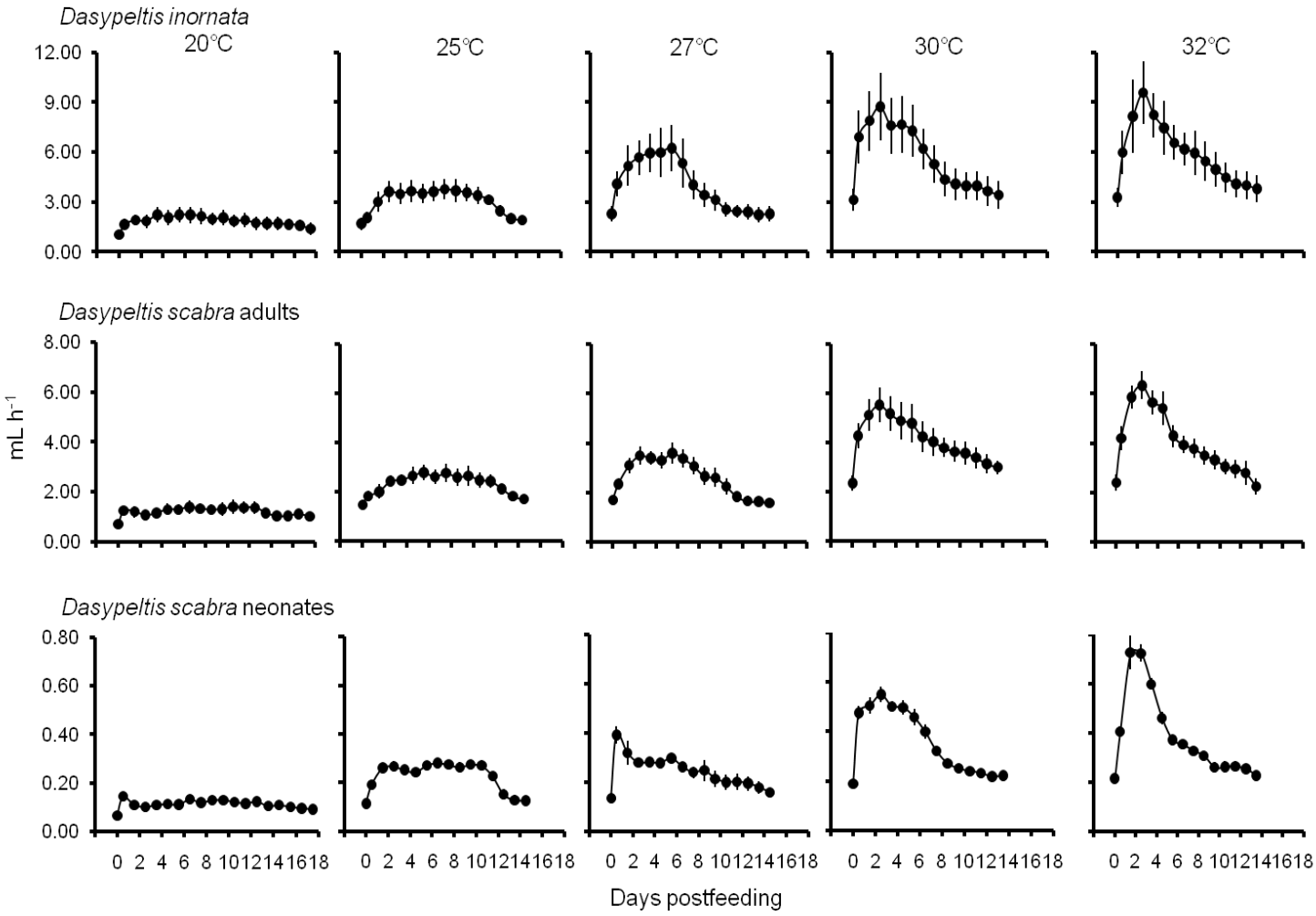


Figure 2.1 Mean VO_2 (ml O_2 h^{-1}) of *Dasypeltis inornata* and *Dasypeltis scabra* adults and neonates prior to (day 0) and up to 18 days after the ingestion of chicken egg meals equaling 20% of snake body mass at body temperatures (T_b) of 20, 25, 27, 30 and 32°C. For all temperature trials *D. inornata* n = 4, *D. scabra* adults n = 8 - 10, *D. scabra* neonates n = 8 - 11. Error bars represent ± 1 SE. Note that with an increase in T_b after feeding, oxygen uptake is elevated and the SDA response is shorter.

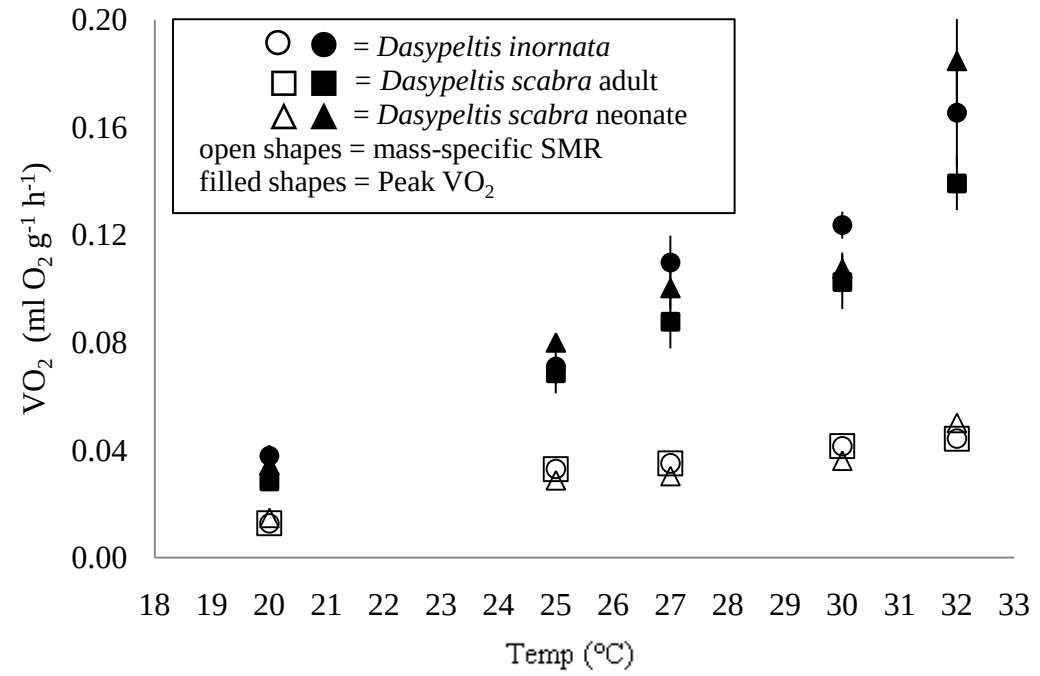
2.4.2 Inter- and Intraspecific Comparison

With few exceptions, metabolic variables measured did not vary significantly between *D. scabra* adults and *D. inornata* at each temperature. Mass did not vary significantly between the two groups at any temperature; therefore, significant results of ANOVA and ANCOVA are reported for whole-animal and mass-specific metabolic variables. At 20°C, mass-specific MR varied significantly ($F_{1, 10} = 5.7261$, $P = 0.0378$), while peak VO_2 (ml O_2 g^{-1} h^{-1}) was borderline significant ($F_{1,10} = 4.6683$, $P = 0.0561$). Peak VO_2 (ml O_2 h^{-1}) was significantly different between the two groups at 27°C ($F_{1, 11} = 5.1539$, $P = 0.0443$) and 30°C ($F_{1, 9} = 5.2887$, $P = 0.0470$). Mass as the covariate was highly significant and accounted for much of the variation at both 27°C ($F_{1, 11} = 12.2066$, $P = 0.0050$, $r^2 = 0.52$) and 30°C ($F_{1, 9} = 35.5811$, $P = 0.0002$, $r^2 = 0.75$). The exceptions were significantly lower in *D. scabra* adults than *D. inornata* adults (Figure 2.2). While generally not statistically significantly different, *D. inornata* whole-animal and mass-specific mean values for metabolic variables were on average higher than those measured for *D. scabra* adults.

Only mass-specific metabolic variables were compared between *D. scabra* adults and neonates to eliminate the effects of differences in M_b. At 20°C, mass-specific peak VO_2 (ml O_2 g^{-1} $h^{-}1$) varied significantly between adults and neonates ($F_{1, 17} = 5.6873$ $P = 0.0290$). At 25°C, mass-specific peak VO_2 ($F_{1, 15} = 5.5336$ $P = 0.0327$), the factorial scope ($F_{1, 15} = 7.4469$ $P = 0.0155$), SDA (kJ kg^{-1}; $F_{1, 15} = 8.4408$ $P = 0.0109$) and the SDA coefficient ($F_{1, 15} = 8.4408$ $P = 0.0109$) were statistically significantly different between the two groups of snakes. Scope ($F_{1, 19} = 4.3196$ $P = 0.0514$) and mass-specific peak VO_2 ($F_{1, 15} = 4.1806$ $P = 0.0589$) were also borderline significantly different at 27°C and 30°C respectively. Comparatively, adults exhibited lower mean values of mass-specific peak VO_2, SDA, the SDA coefficient and scope of peak VO_2 (Table 2.1 and Figure 2.2a).

To determine mass exponents, SMR, peak VO_2 and SDA were plotted against M_b for *D. inornata* and *D. scabra* with adults and neonates combined (Figure 2.3). Body temperature and meal size were held constant at 30°C and 20% of body mass respectively. SMR scaled with a mass exponent of 0.94 for *D. inornata* and 1.03 for *D. scabra* (Figure 2.3). Peak VO_2 and SDA scaled with mass exponents of 1.01 and 0.96 respectively for *D. inornata*. Mass exponents for peak VO_2 and SDA for *D. scabra* were 0.95 and 0.93 respectively. With mass exponents close to 1.00, metabolic rate appears to increase proportionally with M_b for both species and M_b accounts for a significant portion of the variability within MR intraspecifically except for neonates (Figure 2.3).

a.



b.

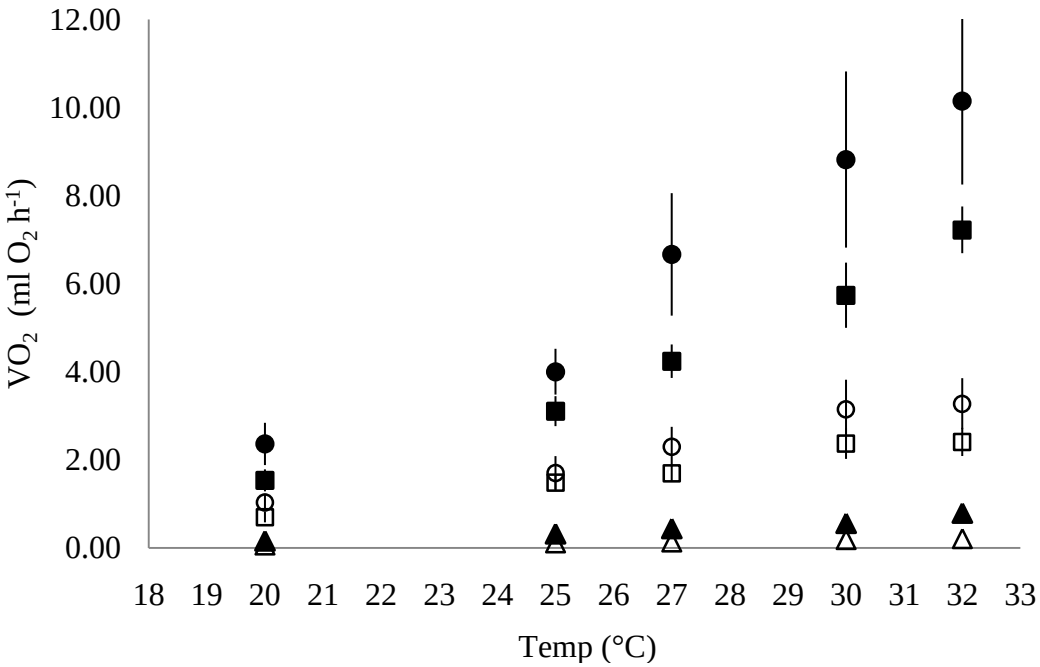
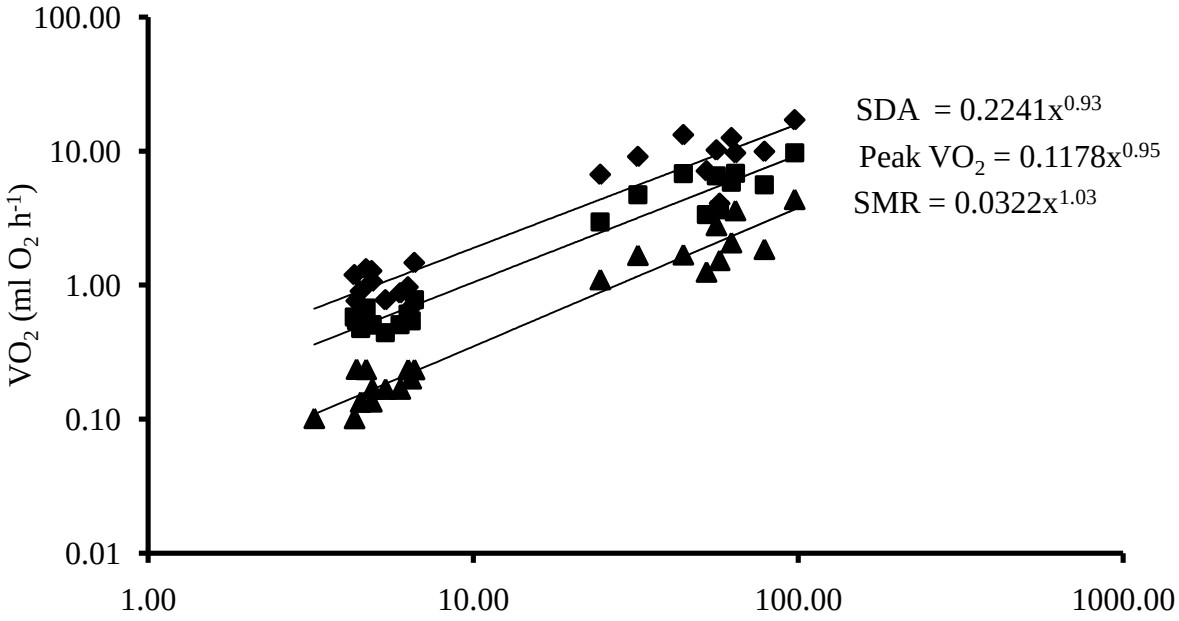


Figure 2.2 a.) Intra- and interspecific comparison of mass-specific standard metabolic rate (SMR; ml O_2 g^{-1} h^{-1}) and peak VO_2 (ml O_2 g^{-1} h^{-1}) plotted for each temperature for *Dasypeltis inornata* and *D. scabra* adults and neonates. b.) Intra- and interspecific comparison of standard metabolic rate (ml O_2 h^{-1}) and peak VO_2 (ml O_2 h^{-1}) plotted for each temperature for *Dasypeltis inornata* and *D. scabra* adults and neonates. Note *D. inornata* SMR (○), *D. inornata* peak VO_2 (●), *D. scabra* adult SMR (□), *D. scabra* adult peak VO_2 (■), *D. scabra* neonates SMR (△), *D. scabra* neonates peak VO_2 (▲). Error bars that cannot be seen outside of the shape have been omitted.

a. *Dasypeltis scabra*



b. *Dasypeltis inornata*

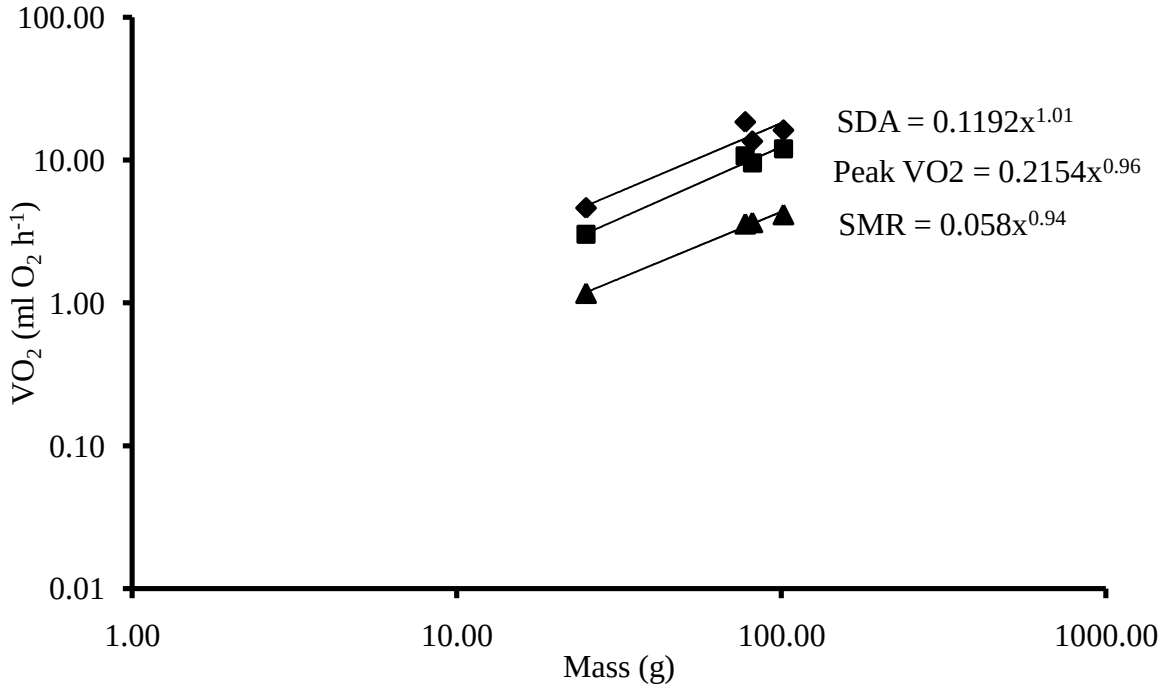


Figure 2.3 Peak VO_2 (ml O_2 h^{-1}), SMR (ml O_2 h^{-1}) and SDA (kJ) plotted against body mass (g) on a $\log_{10}$ - $\log_{10}$ scale for (a.) *Dasypeltis scabra* - adults and neonates and (b.) adult *Dasypeltis inornata*. Data were log transformed prior to generation of equations. Data generated for plots originated from experimental trials at 30°C where snakes were fed liquid contents of chicken egg equivalent to 20% of body mass. Note SDA kJ (◆), Peak VO_2 ml h^{-1} (■), SMR ml h^{-1} (▲).

2.5 Discussion

Dasypeltis inornata and *D. scabra* adults and neonates exhibit a metabolic response similar to infrequently feeding snake species (Ott and Secor 2007a; Secor and Diamond 2000; Zaidan and Beaupre 2003) including up-regulation of the gastrointestinal tract (Bramwell 2006; Groβmann and Starck 2006). The metabolic response also included a significant rise in VO_2 after feeding and a peak in VO_2 normally within 48h of meal ingestion. Thereafter, oxygen consumption returned to resting levels at a slower rate (see Secor 2009 for diagrammatic representation of a typical response). Results also suggest that digestive response in both *D. scabra* adults and neonates and *D. inornata* are thermally sensitive and digestive duration and energy expended during digestion vary with changes in T_b.

Current studies typically compare SDA among snakes at 25°C and 30°C and a meal size ranging from 20 – 25% of M_b (Ott and Secor 2007b; Toledo et al. 2003; Zaidan and Beaupre 2003). Yet, many species encounter much higher temperatures and may select higher T_b than 30°C for digestion through behavioural thermoregulation and microhabitat selection (Alexander et al. 2001; Regal 1966; Slip and Shine 1988b). Inclusion of a higher maximum trial temperature up to 35°C may be appropriate in future digestive studies for *Dasypeltis* species.

Although not all snakes are effective thermoregulators and may fail to show postprandial thermophily (Rice et al. 2006), the efficacy of thermoregulation can affect digestive function (Cowles and Bogert 1944). The thermoregulatory ability and preferred T_b for digestion for *D. scabra* and *D. inornata* is unknown. Differences observed in digestive duration across trials (Table 2.1) may indicate that *Dasypeltis* species are more efficient at digesting at higher T_b and may select a temperature above 32°C for optimal digestion. Previous studies show that the duration of the metabolic response to feeding ranges from two days for the frequently feeding snake *Thamnophis sirtalis* (Peterson et al. 1998) to 12 days for the ambush forager *Crotalus cerastes* (Secor and Diamond 2000). A meal equivalent to 25% of M_b at 30°C takes an average of 7 ± 0.4 (n = 24) days to digest while a meal equal to 20% of M_b at the same temperature requires an average of 5.4 ± 1.3 days to digest (n = 3; calculated from data in Secor 2009 excluding Groβmann and Starck 2006 study). These figures are, however, based on a number of infrequently feeding species that typically consume large meals (> 50% of M_b) of intact prey items containing bone and/or fur. The digestion duration for *D. inornata* fell within the range of other

species at the same temperature and meal size and was 2-3 days shorter than digestive duration of *D. scabra* adults and neonates. For a meal equivalent to 20% of body mass at 30°C, the duration of the digestive response for *D. scabra* adults and neonates was 9.5 and 8.5 days, respectively. Groβmann and Starck (2006) found that *D. scabra* needed on average of 11 days to digest a meal of the same size at the same temperature. Adult and neonate *D. scabra* appear to require more time than other snakes to digest a meal of 20% of M_b at 30°C.

Studies have shown prey type and composition can also affect metabolic response (Grayson et al. 2005; McCue et al. 2005; Secor and Boehm 2006; Secor et al. 2007). Consuming ground, cooked or liquid meals has been shown to reduce the digestive effort and the duration of metabolic response relative to the time and energy required for consuming intact prey items (Boback et al. 2007; Christel et al. 2007). Dietary specialists have also been shown to be more efficient at assimilating prey items due to morphological, behavioural and physiological specializations conferring an energetic advantage (Britt and Bennett 2008; Mori and Vincent 2008).

Based on the dietary specialization and the liquid content of the diet of *Dasypeltis*, it was predicted that these snakes would be more efficient at consuming meals in terms of duration of digestion and overall energy required to digest prey items. It was expected that *Dasypeltis* would have required less time to digest because liquid meals should require less enzymatic breakdown. While the scope and SDA coefficient for both *Daspyeltis* species are some of the lowest reported for snakes, with similar results reported in Groβmann and Starck (2006), the duration of the metabolic response was longer than expected, but both species of *Dasypeltis* did exhibit lower SDA (kJ kg^{-1}) relative to other species digesting a meal of 20% of M_b at 30°C. The average SDA for other species was 328.56 ± 71.98 (data for other species was adapted from review Secor 2009). SDA (kJ kg^{-1}) for *D. scabra* adults and neonates was 182.49 ± 25.00 and 198.69 ± 17.80, respectively and 186.91 ± 17.92 for *D. inornata*. *Dasypeltis scabra* may take longer on average to digest a meal, but generally, both *Dasypeltis* species appear to use less energy to digest the contents. Whether this decrease in energy expended for digestion is related to meal type or advantages of dietary specialization is unknown.

Longer digestion periods may have associated physiological implications that may, in turn, have implications for energy budgets, reproduction, foraging and growth in the individual. Although most species are capable of consuming another meal during digestion, it is often the case that, during digesting or directly following consumption of a

meal, a snake's movement is curbed leaving less time for foraging (Garland and Arnold 1983; Shine and Shetty 2001). Thus, less foraging may result in less prey encounters and ultimately, less energy intake hindering growth. Physiologically, increased digestion duration may point to variation in the capacity and strength of digestive secretions to break down a meal even in liquid form. Although some snakes consume intact prey, shorter digestion durations because of increased strength in enzymatic breakdown or other physiological variation may confer digestive advantages.

The ability to assimilate more energy or to minimize the amount of energy spent digesting a meal relative to the energy consumed would have added advantages (Lillywhite 1987) particularly for snakes that encounter seasonally available prey items. Energy saved on digestion can be used elsewhere during periods of low prey availability. Although *Dasypeltis* species are considered active foragers, due to the seasonal availability of avian eggs, feeding bouts may range from intermittent during winter months to abundant feeding during peak egg-laying months. The annual variability in prey availability may increase selective pressures to conserve energy. The lower SDA coefficient of *Dasypeltis* species relative to other snakes suggests that less energy is being spent on digestion relative to that consumed. The conservation of energy during digestion may allow for allocation to increased foraging time when prey is not readily abundant, or in the case of neonates for growth. Furthermore, down-regulating the gastrointestinal tract in *Dasypeltis* may also help to conserve energy between meals and during longer fasting periods (Bramwell 2006; Groβmann and Starck 2006).

2.5.1 Body Temperature, Age and Species Effects

Increases in T_b resulted in increases in metabolic variables including SMR, peak VO_2 and SDA when holding meal type and size constant, a pattern consistently seen in other species (McCue and Lillywhite 2002; Secor and Faulkner 2002; Skoczylas 1970; Zaidan and Beaupre 2003). In all *Dasypeltis* groups, as T_b increased, peak VO_2 and SMR increased at proportionally similar rates. At higher T_b, peak VO_2 was reached within 72h of meal consumption, which is slightly longer than other species (Andrade et al. 1997; Hopkins et al. 2004; Secor 2003). At T_b below 27°C, peak VO_2 was less distinct and the rapid rise in oxygen consumption was minimal for all groups resulting in relatively flat postprandial metabolic responses and a longer duration of digestion. There were few significant

differences between digestive metabolic scopes except between the lowest and the highest trial temperatures for *D. scabra* adults and neonates.

Increased T_b led to increases in minimum maintenance (SMR) and digestive costs (SDA). At temperatures of 30°C or higher, digestion is energetically costly, accounting for 12 – 16% of the total energy consumed, similar to other species (Andrade et al. 1997; McCue et al. 2005). Although maintenance and feeding at higher temperatures is more energetically costly, many species do behaviourally select for increased T_b during digestion (Beck 1996; Sievert et al. 2005; Touzeau and Sievert 1993). Selecting for increased T_b during digestion may be related to decreasing digestive duration during periods of prey abundance, but not necessarily to increasing digestive efficiency (Greenwald and Kanter 1979; Wang et al. 2003). In ecologically relevant terms for *Dasypeltis* species, increased temperatures coincide with prey abundant periods during summer (peak egg laying season). *Dasypeltis scabra* and *D. inornata* may exhibit postprandial thermophily to capitalize on consuming large numbers of eggs while they are more abundant. Further thermoregulatory studies are needed to determine if *Dasypeltis* species 1.) effectively thermoregulate, and the preferred T_b or set point range and 2.) exhibit postprandial thermophily.

At lower temperatures, SDA appeared to be less costly in terms of energy expended to digest. In the case of *Dasypeltis* species, 20°C is not outside of the relevant ecological temperatures that would normally be experienced in early spring, late fall or winter months. If *Dasypeltis* feeds in any of these months, even rarely, then they would have the capacity to digest a meal at 20°C, but the process may be hindered or not as effective in extracting energy from the meal as at higher T_b. While snakes did not regurgitate the meals and defecation did occur, in some instances up to two weeks after feeding (pers. obs.), the amount of digestion taking place was most likely less than at higher T_b. The result looks like "cheaper" digestion at lower T_b, but may simply be the result of digesting less of the meal. Some species are not able to digest at this temperature and simply regurgitate the meal indicating digestion was arrested at 20°C (Wang et al. 2003), but not for *Dasypeltis*. The ability of *Dasypeltis* species to digest meals at lower T_b may be related adaptive traits over an evolutionary time frame or simply because the enzymatic breakdown required to digest a liquid meal is less than one containing bones and fur.

The metabolic response for *D. inornata* and *D. scabra* is lower than other active foragers and ambush foragers (Table 2.2) and was, in fact, one of the lowest postprandial metabolic responses recorded for snakes. The lower scope and SDA (kJ) is related to a

reduction in the energy and effort required to initiate gastric breakdown, nutrient catabolism and biosynthesis of a liquid meal (Christel et al. 2007; Coulson and Hernandez 1979; Secor 2009). Other snake species that were fed intact rodent meals of the same size (20 – 25% of M_b) and at the same T_b required more energy to digest (Table 2.2; Boback et al. 2007). Overall, other active and ambush foraging snakes had metabolic scopes that were at least double that of the *Dasypeltis* species tested. The digestive effort in other species requires a larger proportional increase in energy expenditure above SMR to complete digestion (Secor 2009); which suggests that, foods higher in energy content, more frequent feeding bouts or larger meals are required to satisfy the energy demands related to increased gastric breakdown costs.

To date few studies have tested digestive efficiency between an intact meal and an egg meal, but preliminary results suggest that meals consisting of the yolk and albumen of eggs require less energy to digest than intact rodent meals. Christel (2007) found that the Gila monster, *Heloderma suspectum*, used 24% less energy to digest and assimilate the liquid contents of an egg than an intact rodent meal of equal mass. Metabolic scope was 19% less for *H. suspectum* digesting egg versus an intact rodent meal (Christel et al. 2007). While *H. suspectum* can weigh 5 to 10 times that of an average adult *Dasypeltis*, the metabolic variation for digesting an intact rodent meal and an egg meal emphasizes the variability in costs associated with digesting different meal types. For a meal of only 10% of M_b, *H. suspectum* used 43.2 kJ to digest and assimilate the egg (Christel et al. 2007), whereas, *D. inornata* and *D. scabra* used only 13.18 and 9.90 kJ, respectively for a meal equivalent to 20% of M_b. Although meal sizes would be very different because M_b are different between *H. suspectum*, *D. scabra* and *D. inornata*, as a proportion of total body size, *Dasypeltis* species used less energy to digest the same meal type.

Pre- and postprandial metabolic response can vary due to ontogenetic differences, and may influence the energy expended for digestion. Neonates can exhibit higher metabolic rates presumably as a cost to synthesize new tissues (Beaupre and Zaidan 2001). In this study, mass-specific SMR and SDA generally, did not differ significantly between adults and neonates but mass-specific peak VO_2 was greater for neonates than adults. Neonates also used more energy during digestion relative to that consumed as their SDA coefficients were on average 17% higher than adult SDA coefficients. While energy expended during digestion was greater across all temperature trials for neonates, differences may be the remnant of ratio calculations and mass scaling relationships.

Increased postprandial MR in younger animals is common as more energy is expended for the purposes of rapid growth, but there is conflicting evidence of significant differences in SMR/RMR between adults and neonates (Beaupre and Zaidan 2001; Nagy 2000). Few studies have examined an added "growth cost" during digestion (Beaupre and Zaidan 2001; Nagy 2000). The increased energy expenditure of neonates exhibited in this study may provide preliminary evidence that there is added cost to neonates during digestion related to growth requirements.

Variation between *Dasypeltis* species and between neonate and adult *D. scabra* did occur for some metabolic response variables, but was usually not significantly different. Body mass affected whole animal metabolic measurements, but after factoring out M_b effects by using mass specific metabolic measurements, significant variation inter- and intraspecifically was still minimal. Results for *D. inornata* are, however, preliminary as the small sample size may have skewed the actual metabolic relationship inter- and intraspecifically. Thus, the relationship between mass and certain metabolic response variables (Figure 2.3b) may be less linearly associated, resulting in mass exponents that vary from one. However, the general trend that increases in T_b increase the energy expended for maintenance and digestion but decrease digestion duration is consistent with that observed in other species (Bontrager et al. 2006; McCue and Lillywhite 2002; Toledo et al. 2003; Zaidan and Beaupre 2003).

Finally, it should be noted that the bias created by the method used for determining SDA duration was considered, but while duration estimates may have erred on the shorter side, SDA calculations are technically only supposed to include digestive costs. Including additional energy expenditure not significantly different to SMR levels could lead to inflated costs of digestion, as the point at which digestion stops and maintenance metabolism begins is not easily determined if the noise to signal ratio is limited. If SDA duration were taken as the point of no difference between SMR and SDA, the total energy cost associated with digestion would also include maintenance costs not associated with digestion. In future studies, a possible solution to determining digestive duration could be

to define the end of digestion as the point at which elevated VO_2 is different from SMR by a preselected percent (i.e., 5% difference from SMR; Alexander pers. comm.).[4]

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Table 2.2 Metabolic variables and conditions for SDA studies of various species of snake

Species	M_b (g)	T_b (°C)	Meal Size (% of M_b)	Meal Type	Scope	Duration (Days)	SDA (kJ)	SDA coefficient (%)	Intermittent feeder (I)/ Active forager (A)	Study
Acrantophis dumerili	206	30	25.1	Rodent	7.60	6	67.6	21.9	I	(Ott and Secor 2007a)
Agkistrodon piscivorus	139	25	23.4	Fish	5.70	9.2	37.1	26.5	I	(McCue and Lillywhite 2002)
Boa constrictor	69.8	30	25	Rodent	7.83	6	25.4	29.0	I	(Ott and Secor 2007a)
Boa constrictor	137	30	20	Rodent	3.96	4.8	34.4	16.8	I	(Toledo et al. 2003)
Boa constrictor	346	30	25.1	Rodent	18.50	8	232.0	33.0	I	(Secor and Diamond 2000)
Coluber constrictor	223	30	25	Rodent	5.40	4	68.9	15.0	A	(Secor and Diamond 2000)
Crotalus cerastes	127	30	26	Rodent	7.86	9	60.0	23.0	I	(Secor et al. 1994)
Crotalus cerastes	161	30	25	Rodent	9.90	12	73.2	21.0	I	(Secor and Diamond 2000)
Crotalus durissus	42	30	20	Rodent	3.72	3	7.3	12.2	I	(Andrade et al. 1997)
Dasypeltis scabra	47	30	20	Egg	1.97	11	8.9	13.2	A/I	(Groβmann and Starck 2006)
Dasypeltis scabra	59	30	20	Egg	2.47	9.5	9.9	12.0	A/I	This study
Dasypeltis scabra	47.3	25	20	Egg	2.18	13.5	6.2	8.5	A/I	This study
Dasypeltis inornata	71.3	30	20	Egg	2.76	6.5	13.2	12.3	A/I	This study
Dasypeltis inornata	61.6	25	20	Egg	2.64	13.5	6.0	6.2	A/I	This study
Lampropeltis getula	188	30	24.8	Rodent	7.00	4	56.0	14.0	A	(Secor and Diamond 2000)
Lamprophis fuliginosus	16.3	25	20	Rodent	5.10	6	3.3	14.5	A	(Roe et al. 2004)
Masticophis flagellum	273	30	25	Rodent	5.90	5	70.4	13.0	A	(Secor and Diamond 2000)

Species	M_b (g)	T_b (°C)	Meal Size (% of M_b)	Meal Type	Scope	Duration (Days)	SDA (kJ)	SDA coefficient (%)	Intermittent feeder (I)/ Active forager (A)	Study
Morelia spilota	64.8	30	25	Rodent	8.03	5	15.1	18.7	I	(Ott and Secor 2007a)
Morelia spilota imbricataa	130	30	23	Rodent	6.31	6	52.6	22.1	I	(Thompson and Withers 1999)
Nerodia fasciata fasciata	30.2	25	19.7	Fish	5.64	3.5	5.4	21.1	A	(Hopkins et al. 2004)
Pituophis melanoleucus	732	30	25.1	Rodent	8	5.0	211	14.0	A	(Zaidan and Beaupre 2003)
Python brongersmai	763	30	25	Rodent	11.30	8	322.0	23.1	I	(Ott and Secor 2007b)
Python molurus	300	30	20	Rodent	8.59		118	24.5	I	(Overgaard et al. 2002)
Python molurus	500	30	20	Rodent	6.30	8	248.0	31.0	I	(Wang et al. 2003)
Python molurus	690	30	25	Rodent	15.30	8	420.0	30.0	I	(Secor and Diamond 1997)
Python molurus	719	30	25	Rodent	14.50	6	317.0	24.5	I	(Ott and Secor 2007b)
Python molurus	736	30	25	Rodent	17.10	8	438.0	29.8	I	(Secor and Diamond 1995)
Python molurus	2394	30	25	Rodent	16.80	8	1259	26.5	I	(Secor 2003)
Python regius	147	30	25	Rodent	5.23	10	51.7	18.8	I	(Starck et al. 2004)
Python regius	147	30	25	Rodent	4.74	9	17.4	6.7	I	(Starck and Wimmer 2005)
Python regius	715	30	25	Rodent	9.90	8	326.0	25.1	I	(Ott and Secor 2007b)
Python reticulatus	730	30	25	Rodent	10.4	7	340	25.6	I	(Ott and Secor 2007b)
Python sebae	706	30	24.9	Rodent	11.70	6	347.0	27.3	I	(Ott and Secor 2007b)

Metabolic variables defined in Table 2.1. Table adapted from review by Secor (2009).

Chapter 3 - Concluding remarks

Understanding the physiology of a species has become an integral part of conservation efforts as the stability of vertebrate populations decreases due to climatic changes and anthropogenic pressures. Through physiological studies, analysis of the extent of variability in a trait and the response of particular traits to environmental changes can provide a comprehensive understanding of the adaptability potential or potential tolerance to temperature changes (Piersma and Drent 2003). In large part, species are unable to cope with and adapt to current climatic changes because of the rapidity with which changes are occurring (Pullin 2002). Species at highest risk face not only anthropogenic pressures, but may also have limited distributions, low population densities and population limiting life-history traits such as low fecundity and slow growth rates (Purvis et al. 2000). Highly specialized and rare species also face higher extinction risks because of inherent limitations for suitable alternatives (Boyles and Storm 2007; Foufopoulos and Ives 1999; Julliard et al. 2004; Sorensen and Dearing 2004). Climatic changes may include increases in seasonal temperatures. While negative for some species, increases in environmental temperatures could be beneficial for some ectotherms and more specifically, snakes.

In South Africa, it is predicted that mean ambient temperatures could rise by 2°C by 2050 (Erasmus et al. 2002). Many reptiles are effective thermoregulators through behavioural (Anderson et al. 2005; Avery 1982; Bennett 2004) and physiological means (Brown and Au 2009; Tattersall et al. 2004) and have wide thermal tolerances (Alexander et al. 1999), such that a 2°C increase in ambient temperature would most likely have little negative effect on most species. In fact, thermoregulatory behaviour is closely linked to optimizing digestive performance and energy gain (Angilletta et al. 2002a). Digestive performance is, in turn, sensitive to changes in body temperature (T_b; Angilletta et al. 2002a; Greenwald and Kanter 1979), and is often optimized at higher selected T_b (Beck 1996; Slip and Shine 1988b). Reptilian species that are not as effective at thermoregulating may also benefit from increases in T_a as passive conformity to higher T_b may optimize or improve various performance functions at a lower energetic cost (Huey and Slatkin 1976).

Dasypeltis scabra and *D. inornata* both exhibited increased digestive performance (i.e. shorter digestion durations) at higher T_b. Additional studies to determine their preferred T_b or range of preferred T_b (T_{set}; Hertz et al. 1982) would provide a better

understanding of how increased T_b would affect digestive performance and what T_b optimizes digestive performance. A thermoregulatory study could also determine if *Dasypeltis* species exhibit postprandial thermophily. It is possible that a 2°C increase in T_a would have no effect on *Dasypeltis* species if they are effective behavioural thermoregulators. Even if *Dasypeltis* are passive thermoconformers, if available T_a allow for selection of habitats that lead to higher T_b, optimization of digestive performance would still be possible via thermoconformation.

While physiological performance in *Dasypeltis* may not be hindered by small increases in T_a, bird breeding seasons and egg-laying is expected to be change because of climate changes. Climatic changes in temperature can cause either shifts in peak egg-laying season or variation in clutch size, regardless if it is related to microevolutionary adaptation or phenotypic plasticity (Dunn 2004; Winkler et al. 2002). Breeding is occurring earlier and migrant species are migrating sooner (Both et al. 2004; Cotton 2003; Walther et al. 2002). Reductions in bird populations and local extirpations are also possible due to climate change (Simmons et al. 2004; Wichmann et al. 2003), which could certainly affect the number of eggs available for consumption by *Dasypeltis*. Indirectly then climate change may affect the availability of prey for *Dasypeltis*. If birds breed earlier and egg-laying season occurs sooner, prey will be abundant during periods of colder temperatures. Selection of higher T_b may not be possible depending on how early the egg-laying season occurs. If the egg-laying season advances relatively little, changes in available temperatures during prey abundance will be minor and most likely insignificant. In areas where *Dasypeltis scabra* and *D. inornata* distributions overlap, competition may also increase as a result of the increased demand for scarce resources if bird populations and, in turn, the number of available eggs are reduced.

At higher T_b, *D. scabra* and *D. inornata* used more consumed energy for digestion leaving less energy available for other functions. While the energy required to digest the egg meal at 20°C was substantially less than that at 25 or 30°C for both *D. scabra* and *D. inornata*, the probable cause was that the snakes were digesting less of the food. Thus digestion was actually more costly because net energy gained from digestion was less than that at higher T_b. While less consumed energy is spent on digestion at lower T_b (smaller SDA coefficient), the duration of digestion is extended. If the time to digest a meal is extended, more time is taken to extract essential nutrients and assimilate energy. Longer digestion and assimilation times translate into less energy being immediately available for other vital functions including continued foraging and reproduction.

The thermal dependence of metabolic rate (MR) is clear as changes in T_b affected the pre- and postprandial metabolic performance of each group. Higher T_b led to decreases in digestion duration suggesting that the optimal temperature (T_o) for digesting quickly is at or above 32°C. The preferred T_b (T_{sel}) for *Dasypeltis* species may vary within a larger range, however, because optimization of different functions occurs at different times depending on the circumstances the individual is faced with in the environment including, reproductive status, predator abundance and resource availability. Since the thermal optima vary, T_{sel} may vary to maximize specific functions at different times or will be constant allowing multiple processes to function at a moderate but not optimal level (Angilletta et al. 2002a). The variation in performance also suggests that there is phenotypic flexibility in MR and some level of plasticity which affords adaptive responses to changes in climate conditions. The distinct trophic specialization in *Dasypeltis* species may, however, hinder the level of flexibility for MR.

Results of this study which identify some benefits to specializing on egg-eating (liquid contents) are preliminary, but do suggest that there is less energy expended to digest egg yolk and albumen as a result of a reduction in enzymatic breakdown. If eggs are available, selective pressure should maintain or increase the level of dietary specialization further increasing digestive efficiencies and reducing energy expenditure. Future studies comparing other facultative oophagous species will determine whether *Dasypeltis* species gain an energetic advantage over other species by specialized feeding behaviour and consuming only liquid meals. Determining minimum metabolic energy requirements in all trophic guilds of snake is most important because if minimum maintenance requirements are not met, there will be an energy shortage for carrying out other processes (Zaidan 2003). Physiological studies are therefore essential in forming a comprehensive understanding of a species niche and its adaptive capacity to environmental changes (Garland and Adolph 1991).

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