Autecology of the rhombic egg-eater, *Dasypeltis scabra*

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Declaration

I, Jody Michael Barends, declare that this thesis is my own, unaided work. The contents of this thesis have not been submitted before for any other degree or at another university other than the University of the Western Cape.

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Student number: 3263528

20 June 2022

"Eggberta", an adult egg-eater (*Dasypeltis scabra*) from Milnerton Racecourse Nature Reserve, Cape Town, South Africa.

“It appears that a look at groupings of adaptations in individual species or assemblages of organisms forces one to establish a completely different way of evaluating problems. It may help to develop distinct questions and perhaps lead to distinct answers. In any case, it will help to unravel the ‘interesting’ specialization of the animals about us. The time has probably never been more opportune for approaching such issues. Our interests may well be expanding, but the extent and diversity of the geographical regions capable of supporting our studies are diminishing hourly, as human ‘progress’ continues to reduce organismic diversity around the world.”

– Carl Gans (1978). All animals are interesting. *American Zoologist* 18: 3–9.

Abstract

Efforts to prevent global losses of biodiversity are hindered by incomplete knowledge of the functional importance of species. In part, this is due to a paucity of information on the basic biology of most species resulting in a poor understanding of their ecological roles. Snakes represent a speciose group of carnivorous predators that are likely important ecological components of a variety of environments given their roles in modulating the sizes of the populations of their prey. Unfortunately, the ecological importance of most species of snakes has yet to be empirically demonstrated, particularly in native systems.

The aim of this thesis was to increase the body of knowledge regarding the ecology of *Dasypeltis scabra*, the rhombic egg-eater, a bird egg specialist snake species that occurs throughout most of sub-Saharan Africa. These snakes potentially play an important role in ecosystem functioning by modulating bird recruitment through the predation of bird eggs. However, beyond broad generalizations of their obligate bird egg diets, surprisingly little is known of the feeding habits of *D. scabra*, making it difficult to robustly quantify their impact on bird populations, and thus ecosystem dynamics. In this thesis, I answer several questions regarding the evolution and foraging ecology of *D. scabra* to provide novel knowledge that may assist in informing an understanding of the functional importance of these snakes.

Firstly, to contextualize bird egg consumption by snakes, and bird egg specialization by *Dasypeltis scabra*, I reviewed published and unpublished records of avian oophagy by snakes globally. Avian oophagy by snakes appears to be uncommon, as records of snakes eating bird eggs suggest that < 4% of snake species utilize these prey. Most published records of avian oophagy belonged to *D. scabra* as the eggs of at least 40 species of birds have been reported as prey of these snakes. To investigate the origins of bird egg specialization in *D. scabra*, I explored the evolution of diet, habitat, and body size within the colubrine clade containing

Dasypeltis and their close relatives ―*Boiga*, *Coelognathus*, *Crotaphopeltis*, *Dipsadoboa*, *Gonyosoma*, *Lycodon*, *Telescopus*, and *Toxicodryas*. My results suggest that transitions to dietary specialization and decreased body size in *Dasypeltis* occurred in concert with a shift in the African landscape from closed to open environments during the Oligocene and Miocene epochs.

Next, using a colony of captive *Dasypeltis scabra* housed under laboratory conditions, I calculated the bulkiest eggs that individuals of varying sizes, ranging from newly hatched neonates to large-sized adults could ingest. Using those estimates, I calculated that adult *D. scabra* could feasibly ingest the eggs of 98% of breeding birds in southern Africa, and hatchlings could ingest up to 50%. However, snakes required meals equalling just 61% of their body mass annually to maintain body condition. Snakes accepted food more frequently in warmer months when eggs are abundant and fasted during colder months when eggs are absent. These results suggest that *D. scabra* likely adapted to feeding seasonally which may have led to them evolving low maintenance requirements. I hypothesize that these findings indicate that *D. scabra* likely evolved to an optimal body size since theoretically larger individuals would not gain a demonstrable advantage in prey access and would be disadvantaged by increased yearly feeding needs.

The small body size of *Dasypeltis scabra* has several important implications for their population ecology and community dynamics. At Koeberg Private Nature Reserve, I estimated that *D. scabra* occur at high densities (~5 – 8 snakes ha^{-1}) similar to those of other small-bodied southern African snakes. However, due to their unique diet, *D. scabra* does not compete with small-bodied species and instead competes with much larger snakes (*Dispholidus typus*, *Naja nivea*, and *Pseudaspis cana*) that outsize them but probably occur at lower densities. Consequently, *D. scabra* likely outcompetes its rivals via exploitative competition of bird eggs, and in so doing exerts intensive pressure on bird recruitment.

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Firstly, to my supervisor Dr. Bryan Maritz. You have been an inspiration and role model for the entirety of my graduate career. The constant stream of support, encouragement, ideas, and enthusiasm that you've provided has contributed immensely to the completion of this project. The number of times I've said "thank you" after you've helped with administrative issues, oversaw logistical challenges, or provided feedback is surely in the thousands. Here is one more: thank you for introducing me to the world of herpetology. I am proud to have been the first doctoral candidate under your supervision. Many more will undoubtedly follow.

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Chapter 1: General Introduction

1.1 Biodiversity loss and ecosystem functioning

Biodiversity loss across the globe is at an all-time high and represents a pre-eminent problem of the modern era (Cardinale et al. 2012; Hooper et al. 2012; Lamkin & Miller 2016). In particular, extinctions of species at the hands of human activity, both directly and indirectly, have never been more prevalent (Myers et al. 2000; Mace et al. 2018). Moreover, thousands of species remain threatened or at risk of extinction (Cox et al. 2022). Anthropogenically induced climate change and habitat transformation have defined the current, so-called age of the ‘Anthropocene’ and are hugely responsible for the loss of numerous lineages of organisms and the irreversible collapse of several ecosystems (Clavel et al. 2011; Chase et al. 2020). What was once a proverbial elephant in the room has long since become a bull in a China shop that can no longer be ignored as ever-increasing rates of human population growth and consumption continue to threaten the natural world.

As biodiversity continues to decline at accelerated rates (Stork 2010), ecologists have become increasingly concerned with understanding the consequences of species loss. Research from the past decade has produced a mounting body of evidence showing that species declines have major implications for the processes that sustain the world’s ecosystems (Hooper et al. 2012; MacDougall et al. 2013; Mace et al. 2018; Chase et al. 2020). Different species contribute at varying degrees to important ecological processes such as carbon storage, energy transfer, nutrient and water cycling, and productivity (Hooper et al. 2005; Májeková et al. 2016). Accordingly, the loss of species and their respective ecological contributions can fundamentally and irreversibly change those processes (Laureto et al. 2015). In general, such changes are predicted to exacerbate cascading losses of biodiversity and ultimately cause ecosystem collapse (Hooper et al. 2012; Gascon et al. 2015; Chase et al. 2020).

One approach to stem cascading loss of species is to target and prioritize ecologically important species for conservation. Over the past few decades, many scientists and conservation practitioners have adopted a functional value approach to biodiversity conservation. With this approach, species are evaluated based on their contributions toward ecosystem services that benefit humans and their ecological roles in sustaining ecosystem health (Rosenfeld 2002; Gascon et al. 2015). Theoretically, species deemed essential for ecosystem survival should therefore be given greater priority in terms of conservation effort. For example, species that perform unique ecological roles provide important diversity that prevents functional homogenization (Futuyma & Moreno 1988; Devictor et al. 2008; Mouillot et al. 2011) and thus promotes productivity and complementarity of ecosystems (MacDougall et al. 2013). Under the functional value approach, these functionally unique species would be afforded greater resources for their conservation, creating a knock-on effect in which other associated species are also protected.

While functional biodiversity valuation has shown promise toward benefitting species survival (Rands et al. 2010), one problem with this approach is that the ecological roles and contributions of most species are still unknown (Bengtsson et al. 2000; Hooper et al. 2005; Gascon et al. 2015). Currently, we lack knowledge of the foundational biology, behaviour, and ecology of most species (Gascon et al. 2015). Consequently, the importance of many organisms remains enigmatic and their functional roles are only poorly understood (Mouillot et al. 2011; Májeková et al. 2016). This is a major cause for concern for conservation because how can we evaluate the importance of species if we do not understand their basic ecology?

1.2 The functional roles of snakes in ecosystems

Snakes represent a taxonomic group that has historically received limited attention within ecological research (Shine & Bonnet 2000; Böhm et al. 2013). Relative to other vertebrate groups, including other reptiles like lizards, research on snakes within the fields of ecology and animal behaviour has been disproportionately lower in terms of the number of published studies (Shine & Bonnet 2000). This has been especially prevalent in politically unstable geographical areas like many countries in Africa (Tolley et al. 2016) where, until recent decades, studies on snake ecology have been virtually non-existent (Branch 1998; Bates et al. 2014). A consequence of this is that many species of snakes have often been overlooked or undervalued as important ecosystem components (Willson & Winne 2016).

The rise in studies of the functional ecology of snakes in recent years (for example Beaupre & Douglas 2009; Willson & Winne 2016; Godley et al. 2017) has begun to highlight the importance of snakes within ecosystems. Predators are essential to ecosystem health (Estes et al. 2011) and all of the approximately 4000 (Uetz et al. 2021) living species of snakes are carnivorous (Greene 1997; Cundall 2019). Collectively, snakes feed on a wide array of prey ranging from minuscule invertebrates to large mammals (Cundall & Greene 2000). Moreover, the diversity and complexity of snake diets across species, populations, and even individuals create important functional diversity within ecosystems (Grundler 2020; Maritz et al. 2021b). Snakes are therefore likely to occupy multiple, and possibly unique, functional groups within several ecosystems. Moreover, snakes may also provide important functional redundancy to other functional groups, thus promoting ecosystem resilience.

Through their capacity as predators, snakes can affect a variety of ecosystem processes in the systems in which they occur through top-down trophic interactions. Most obviously, snakes have the potential to directly modulate and suppress the populations of their prey (Campbell et al. 2012; Dorcas et al. 2012). Although snakes are among some of the most cryptic and secretive species (Durso et al. 2011), they can occur at extremely high densities (for example *Liodytes alleni* occur at densities of > 1200 snakes ha^{-1} in Florida wetlands, Godley 1980) and thus may have a large impact on survival and recruitment rates of their prey. Moreover, predation by snakes can indirectly affect a range of other organisms. Two striking examples of invasive species highlight the above. Intensive predation of birds by invasive brown tree snakes (*Boiga irregularis*) on Guam has facilitated a trophic collapse on the island as snakes hunted several species to extinction or local extirpation, causing declines in seed dispersal rates (Rodda & Savidge 2007; Rogers et al. 2017). In the Florida Everglades, invasive Burmese pythons (*Python bivittatus*) have contributed to severe declines in local mammal populations, leading to improved nesting success of several species of turtles due to reduced predation of eggs by mammals (Willson 2017). Unfortunately, the impacts of snakes in their native systems have not been well-studied and, in many cases, remain subject to speculation. However, given the high species richness of snakes, the diverse nature of their diets, their potential to occur at high densities, and their ectothermic physiology that fundamentally differs from endothermic predators, it is likely that many of these species play important and possibly unique roles as predators in several ecosystems.

1.3 The functional importance of *Dasypeltis*

African egg-eaters of the genus *Dasypeltis* are dietary specialists that obligately feed on bird eggs and do not consume any other types of prey (Branch 1998; Bates & Little 2013). These snakes have evolved a suite of morphological and physiological adaptations that facilitates the consumption of bird eggs and allow for extraordinary feats of ingestion (Gans 1952; Gans 1974). These adaptations include a lack of traditional teeth within the buccal cavity and extremely stretchable tissue between the labial scales and mandibles that allow these snakes to engulf and ingest large bird eggs with apparent ease (Gans 1952; Branch 1998; Gartner & Greene 2008). Moreover, egg-eaters generally do not swallow eggs whole and instead use extensions of their vertebral hypapophyses to breach ingested eggs which they then crush and drain within the oesophagus before regurgitating the egg shell remains (Gans 1952; Gans 1974; Gartner & Greene 2008). The specialized approach to feeding makes these snakes highly proficient at consuming bulky bird eggs.

The highly specialized diet of *Dasypeltis* makes these snakes ideally suited for investigating the impacts of native snakes on prey populations. Many species of birds act as important ecosystem engineers that prominently influence habitat structure through landscape-altering processes like nest production, seed dispersal, and pollination (Whelan et al. 2008; Floyd & Martin 2016; Michel et al. 2020). Additionally, birds provide several ecosystem services that are beneficial to humans (Whelan et al. 2015). Several studies suggest that these snakes are the predominant nest predators in southern Africa (reviewed by Bates & Little 2013). Intensive predation of bird eggs by *Dasypeltis* and the resultant modulation of bird recruitment could thus potentially have a large impact on those processes with important consequences for ecosystem functioning. However, several facets of the foraging ecology of most species of *Dasypeltis* are unknown, making it difficult to robustly assess the effect of predation by these snakes on bird populations, and thus their functional importance remains unclear.

1.3.1 *Dasypeltis scabra* as a model species

For this project, I investigated the evolution and ecology of the rhombic egg-eater, *Dasypeltis scabra*. The biology of this species makes them an ideal model for ecological research within the context of African ecosystems for several reasons, including:

Abundance/availability – *Dasypeltis scabra* is the most widespread member of its genus (Bates & Broadley 2018), occurring throughout most of southern and East Africa (Bates et al. 2014; Spawls et al. 2018). These snakes are abundant in South Africa where they are easily (relative to other snake species) detectable in some areas, making them ideally suited for field and laboratory studies.

Diet – *Dasypeltis scabra* obligately feed on bird eggs and consume no other prey (Bates et al.

2013), making these snakes ideal for studies involving the links between functional morphology of feeding apparatus and specific prey use, as well as variability in prey availability.

Variation in body size – *Dasypeltis scabra* vary in snout-vent length between approximately 160 – 1000 mm. Moreover, juveniles are nearly two orders of magnitude smaller than adults in terms of body mass, making these snakes a good representative for investigations into intraspecific comparisons involving body lengths and mass as variables.

Captivity – *Dasypeltis scabra* are highly suitable for living in captivity. Individuals are known to live for long periods under captive conditions, with one individual having lived for 31 years (Branch 1998). Thus, these snakes are ideal for long term laboratory-based studies.

Safety – *Dasypeltis scabra* are non-venomous, lack traditional teeth, and offer no harmful threats to human safety, making them ideal for safe experimental use.

1.3.2 Background of *Dasypeltis scabra*

Taxonomy – Linnaeus (1758) originally described *Dasypeltis scabra* as *Coluber scaber* and placed it within the Colubridae. The species was reclassified several times since first described (see Bates & Broadley 2018). Most prominently, Peters (1864) transferred it to the genus *Dasypeltis* as *Dasypeltis scaber*. It was subsequently reclassified to its current taxonomy of *Dasypeltis scabra* by Boulenger (1894).

Distribution – *Dasypeltis scabra* is a widespread species that occurs throughout southern, Central, and East Africa (Bates et al. 2014; Bates & Broadley 2018; Spawls et al. 2018). Its range extends from the southernmost point of South Africa (Cape Town) northwards through the Democratic Republic of Congo and eastwards through Ethiopia and South Sudan (Bates & Broadley 2018; Fig. 1.1).

Habitat – *Dasypeltis scabra* occurs across a range of habitats but is primarily found within grasslands, savannas, and woodlands (Bates et al. 2014; Bates & Broadley 2018). The species is absent from deserts (Branch 1998).

Reproduction – *Dasypeltis scabra* is oviparous. Clutches are usually laid between November and January and incubate for approximately 80 days before hatching (Alexander & Marais 2007). Clutch sizes range from 6 to 25 eggs (Branch 1998).

Activity – *Dasypeltis scabra* typically forage nocturnally (Branch 1998; Alexander & Marais 2007).

Conservation status – At the time of writing of this thesis (i.e. 2022), *Dasypeltis scabra* is categorized as 'Least Concern' on the IUCN Red List (Baha El Din et al. 2021). The species occurs within several large protected areas across its range, including the Kruger National Park in South Africa (Barends et al. 2020), the Kavango Zambezi Transfrontier Conservation Area across Angola, Botswana, Namibia, Zambia, and Zimbabwe (Branch 2018), and Kibale National Park in Uganda (Vonesh 2001).

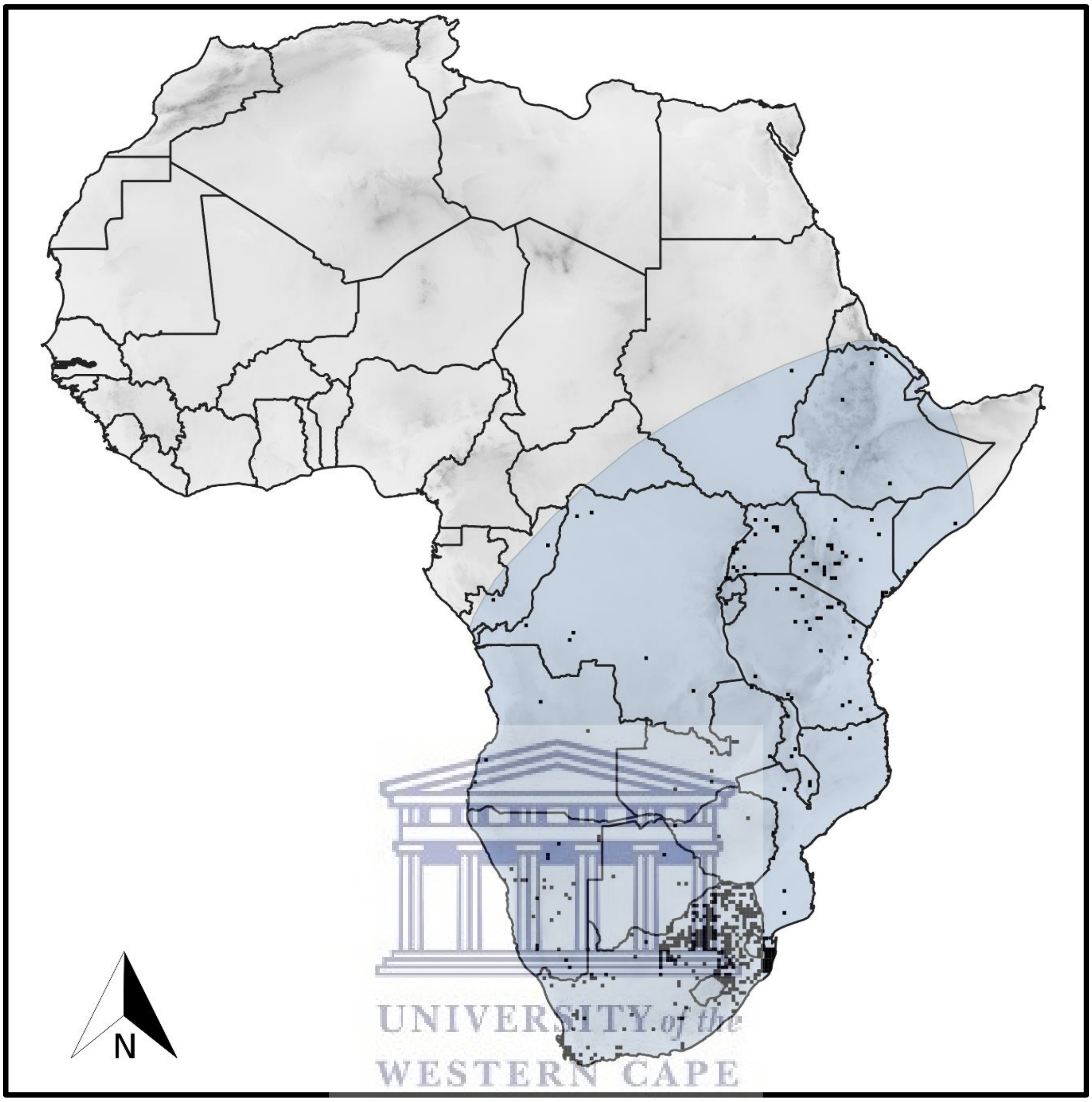

Fig. 1.1: Distribution range of *Dasypeltis scabra* across Africa (shaded in blue). Distribution polygon derived from occurrence points (black squares) available from www.gbif.org.

1.4 Problem statement

Global loss of biodiversity remains at an all-time high and threatens to increase in future (Stork 2010; Cox et al. 2022). A potential negative feedback loop exists in that the loss of functionally important or functionally unique species may incur the loss of others and lead to the collapse of biological systems across a multitude of habitats. Conservation efforts may therefore be expected to prioritize ecologically important species that facilitate ecosystem functioning and sustain productivity. Unfortunately, such efforts are hindered by a lack of knowledge regarding the ecological importance of most species. A case in point is African snake species, many of which likely play vital ecological roles but are poorly studied and thus those roles are unclear. *Dasypeltis scabra* is a widespread species that is potentially hugely important to African ecosystems given the unique predatory role of these snakes as bird egg specialists but a critical evaluation of its functional importance cannot be made until we know more about its ecology.

1.5 Aim

For this project, I aimed to answer several questions relating to the evolution and biology of *Dasypeltis scabra*, and in doing so increase the body of knowledge on the ecology of these dietary specialist snakes. The improved knowledge of the autecology of these snakes can form a foundation upon which robust studies of the functional roles and ecological importance of these, and other species of African snakes, can be built.

1.6 Thesis outline

Excluding this introductory chapter (Chapter 1) and the concluding chapter (Chapter 8), my thesis comprises six stand-alone data chapters that tie together the overarching theme of my research aim. Each of these six data chapters was written independently as an individual study. Consequently, there is some unavoidable overlap in the information presented between chapters. For example, most chapters include descriptions of the unique diet and feeding mechanisms of *Dasypeltis scabra*. Each chapter has been prepared for submission to peer-review journals, some of which have been published. This thesis is structured as follows.

Chapter 2 is a global review of snake predation on bird eggs. I provide a summary of reports of oophagy by wild snakes from across the globe and quantify various facets of these predation events, including geographical biases in predation records and relevant ecological traits of identified oophagous snakes and their bird egg prey. This chapter provides important context for understanding the utilization of bird eggs by snakes as a whole, and thus bird egg specialization by *Dasypeltis*. I provide lists of which species are known to eat bird eggs and which species of bird eggs are eaten. This chapter has been published as “Barends & Maritz (2022a). Snake predators of bird eggs: a review and bibliography. *Journal of Field Ornithology* 93(2): art.1.”

Chapter 3 is an investigation of the evolution of diet and habitat across the clade of Afro-Asian colubrine snakes that includes *Dasypeltis* and their close relatives. I use various ancestral reconstruction analyses to describe the evolution of diets and the development of specialized diets across some of these taxa. This chapter has been published as “Barends & Maritz (2022b). Dietary specialization and habitat shifts in a clade of Afro-Asian Colubrid snakes (Colubridae: Colubrinae). *Ichthyology and Herpetology* 110(2): 278–291.”

Chapter 4 focuses on quantifying spatial and temporal variation of annual food availability for *Dasypeltis scabra* across southern Africa. Through feeding trials of captive snakes, I estimated the maximum ingestion ability of egg-eaters of differing body sizes. I then compared those findings to egg size data for southern African birds to calculate the proportion of potential prey accessible to differently sized snakes, and how those vary monthly. This chapter answers the question of which bird species are at risk of predation by *D. scabra.*

Chapter 5 investigates the annual food requirements and feeding rhythms of captive *Dasypeltis scabra*. I quantified the effect of feeding on snake growth from which I then estimated the minimum yearly food maintenance requirements of these snakes as a function of snake body mass. This chapter answers the question of how many eggs do individual *D. scabra* of different sizes need to consume within a year to survive and grow.

Chapter 6 is a study of the population ecology of *Dasypeltis scabra* at Koeberg Private Nature Reserve, Cape Town, South Africa. I use spatially explicit capture-recapture models to estimate the population density of *D. scabra* at the reserve. These estimates provide important context for understanding the magnitude of the impact of oophagy by *D. scabra* on bird recruitment, and thus the functional importance of these snakes.

Chapter 7 compares the feeding morphology of egg-eaters relative to their closest competitors in southern Africa. I present and compare head size and body size data of museum specimens of *Dasypeltis scabra*, *Dispholidus typus*, *Naja nivea*, and *Pseudaspis cana*. This chapter has been published as "Barends & Maritz (2021). Specialized morphology, not relatively large head size, facilitates competition between a small-bodied specialist and large-bodied generalist competitors. *Journal of Zoology* 315(3): 213–224."

Chapter 8 provides a summary and conclusion to the thesis with recommendations for future avenues of research.

Chapter 2: Snake Predators of Bird Eggs: A Review and Bibliography

This chapter has been published in Journal of Field Ornithology as "Barends, J. M., & Maritz, B. (2022a). Snake predators of bird eggs: a review and bibliography. *Journal of Field Ornithology* 93(2): art.1. https://doi.org/10.5751/JFO-00088-930201"

2.1 Abstract

Snakes are frequent predators of bird nests and therefore potentially have an important impact on bird population dynamics. However, while many species are known to consume nestlings and chicks, few species have been recorded consuming bird eggs. To effectively quantify the effects of bird egg predation by snakes on bird demographics, a key first step is to identify which snake species consume bird eggs. Unfortunately, detailed information on the dietary habits of most snakes is scarce and feeding records are poorly catalogued, making it difficult to ascertain which species do and do not eat bird eggs. I reviewed the literature and online community science reports to compile a global list of confirmed snake predators of bird eggs. In total, I gathered 471 feeding records of 123 snake taxa consuming the eggs of at least 210 bird species from 238 individual data sources. Geographical locations of records disproportionately represented well-sampled regions, and I infer that many snake species not included in my list also consume bird eggs. However, I found that oophagous snakes tend to be long (mean maximum length = 2057 mm) and mostly eat eggs that are small in diameter (mean egg diameter = 24 mm), suggesting that relative prey bulk is an important constraint of these interactions. Therefore, I expect that other snakes that eat bird eggs are likely to mostly include congeneric and ecologically similar species to those reflected in this review. By knowing which snakes consume bird eggs, future research can consider species- and site-specific hypotheses when investigating the ecological effects of bird egg predation by snakes. Those results can also inform conservation practitioners on the causes and consequences of variation in nest success that may aid in decisions when designing conservation management plans.

2.2 Introduction

Predatory attacks by snakes on nesting birds and their offspring have been well-documented globally (for example, in Africa: Lloyd 2004, mainland Asia: Khamcha et al. 2018, Australia: Fulton 2018, North America: DeGregorio et al. 2014, and the Neotropics: Menezes & Marini 2017). However, while many species of snakes are known consumers of nestling birds, chicks, and brooding adults, few species are reported consuming bird eggs. Predation of eggs by snakes can reduce recruitment of birds and impact bird population dynamics (Lavers et al. 2010). In addition, by preying on eggs, snakes have the potential to influence bird life history patterns by forcing them to re-lay and brood successive clutches (DeGregorio et al. 2014). Given that many species of birds provide important ecosystem services (Whelan et al. 2008, Whelan et al. 2015), population fluctuations from reduced recruitment could potentially alter the functional integrity of a range of ecosystems (Mortensen et al. 2008; Gascon et al. 2015; Lowney & Thomson 2021). For example, extensive predation on birds and eggs by invasive brown tree snakes (*Boiga irregularis*) on the islands of Guam has fundamentally altered the local faunal community through extirpation of several species, ultimately causing trophic collapse (Wiles et al. 2003). Thus, by preying on bird eggs in large numbers, snakes have the potential to indirectly influence ecosystem functioning in many biological communities.

Quantifying the extent to which snakes affect ecosystems by consuming bird eggs is hindered by numerous challenges. Several facets of these trophic interactions are unclear, including knowledge of which species of birds lay eggs that are at risk of snake predation, as well as the extent to which predation of bird eggs by snakes varies spatiotemporally (Weatherhead & Blouin-Demers 2004; Lahti 2009; Menezes & Marini 2017). Identification of which snakes consume bird eggs offers a critical first step in understanding these dynamics. Knowing which species of snakes consume eggs allows researchers to formulate predator-specific hypotheses across a range of habitats and environments (Reidy & Thompson 2012; Ibáñez-

Álamo et al. 2015). Additionally, avian conservation practitioners can use that information to produce anti-predator strategies for bird conservation efforts. Unfortunately, information on snake feeding is poorly catalogued (Grundler 2020, Maritz et al. 2021b) making the compilation of a robust list of oophagous species challenging.

Snake diets are diverse, compositionally complex, and often difficult to adequately quantify (Greene 1997; Glaudas et al. 2017; Maritz & Maritz 2020). Unfortunately, the natural history data required to systematically describe snake diets are often lacking, particularly for taxa that occur in poorly-studied regions. For most species, we know very little about their feeding habits apart from generalized characterisations of their diets inferred from a limited quantity of published information (Maritz et al. 2021b). For many others, we lack even a basic understanding of their feeding habits. A recent global synthesis of snake feeding records by Grundler (2020) highlights the incomplete nature of our understanding of snake diets. Of the ~4000 species of snakes distributed across the globe (Uetz et al. 2021), less than a third (1248 species) could be included in that dataset and the majority of those species were only represented by fewer than ten records. Due to this paucity of feeding records, knowledge of the which types of prey are, or are not eaten by different species of snakes is limited. Consequently, many species not currently known to eat bird eggs may be oophagous.

Despite the above limitations, published records of snakes consuming bird eggs have accumulated in the literature (Weatherhead & Blouin-Demers 2004; Ibáñez-Álamo et al. 2015). Over the past few decades, using camera monitoring systems, some snake species have been documented eating eggs for the first time (Cutler & Swann 1999, Pierce & Pobprasert 2007; Ribic et al. 2012; Khamcha et al. 2018). Moreover, novel feeding records published in natural history publications and online community science portals continue to confirm additional species as bird egg predators. However, because studies and platforms vary in their objectives, records are scattered in the literature and online. In some cases, reports may be difficult to access or are completely inaccessible to researchers or conservationists interested in using these data.

I compiled a comprehensive list of confirmed snake predators of bird eggs. I collated records of snakes consuming bird eggs from a range of sources of information and used the details within those reports to broadly summarize trends of bird egg predation by snakes globally. I also analysed several traits of the identified snake species and egg prey to test hypotheses regarding why those species consume bird eggs but many others do not. Specifically, I tested if the inclusion or exclusion of bird eggs in the diets of snakes is associated with 1) differences in snake body size, 2) variation in snake habitat use, and 3) taxonomic relatedness between snake taxa. To contextualize which bird species are at risk, I also compared the size distribution of consumed bird eggs to that of a sample of bird eggs not reported in the diets of snakes. Lastly, I investigated the sizes of eggs consumed by snakes of varying body lengths.

2.3 Methods

2.3.1 Data collection and inclusion criteria

Between August 2020 and July 2021, I searched for and collected data from reports of bird egg predation by snakes. My main sources of data were formal publications (i.e. peer-reviewed journal articles and books) found on the online indexer Google Scholar, JSTOR, and SquamataBase (Grundler 2020) —an online natural history repository containing close to 11 000 records of predator-prey interactions across 1248 snake species. I also searched the literature cited within those publications to identify additional sources. Additionally, I collected data from unpublished academic theses and personal communications from researchers. Lastly, I collected data from community science records published on the online platform iNaturalist (https://www.inaturalist.org) and the social media network Facebook. Facebook records were obtained from the groups “Predation records - reptiles and amphibians (sub-Saharan Africa)" (published in Maritz & Maritz 2020), "Snakes of South Africa" (https://www.facebook.com/groups/snakesofsouthafrica), and "Wild snake predation records" (https://www.facebook.com/groups/wild.snake.predation.records).

I restricted my data collection to include records of snakes unambiguously eating bird eggs. I did not include reports with vague descriptions of snakes attacking nests unless eggs were directly specified as the prey rather than nestlings, chicks, or adult birds. Conservatively, I excluded records without clear evidence of snakes eating eggs. For a record of a snake species to be included it needed to meet these criteria: 1) snakes were observed eating, attempting to eat, or having eaten (shells in digestive tracts) eggs, and 2) records were of snakes in the wild consuming eggs they found without human intervention. I included cases in which the eggs of captive or domesticated birds were consumed if those predatory attacks met the above criteria.

For each reported predation event, I identified the snake and bird species to the finest taxonomic level possible and noted the number of eggs involved. Geographic coordinates were noted from the original record or estimated using Google Maps otherwise. I updated snake species names to match their current taxonomic nomenclature as per Uetz et al. (2021). I provide a summary of these records detailing the taxonomic diversity of oophagous snake predators and their bird egg prey, as well as geographic biases in these trends.

2.3.2 Ecological traits of oophagous snakes and bird egg prey

Although the primary goal of this study was to compile a list of known snake predators of bird eggs, I was also interested in examining traits of those species that might explain why those snakes consume bird eggs but others do not. Differential prey use within a particular snake species is facilitated by several factors, chief among which include varying body size constraints (Arnold 1993; Greene 1997; Maritz & Alexander 2014) and variable encounter rates of different prey (Alencar et al. 2013; Mori & Nagata 2016). Accordingly, I chose to examine and compare the body lengths and primary habitats of the snakes on my list to snakes not known to consume bird eggs. Snake body lengths correlate with their diet breadth as larger snakes can typically consume bulkier and heavier prey than smaller ones, and can therefore hunt a broader range of prey (Arnold 1993; Maritz et al. 2021a; Barends & Maritz 2022b). Habitat use largely influences the probabilities at which snakes encounter different prey (for example, arboreal snakes are more likely to encounter arboreal prey; Harrington et al. 2018). Taken together, these traits are likely major limiting factors towards bird egg consumption by snakes.

Unfortunately, most accounts of snakes consuming bird eggs do not include linear measurements of the sizes of the individual snakes in question. To compensate for this, I instead used maximum body length data (i.e. length from snout to tail) of each species on my list (Electronic dataset S2.1) collected from Feldman et al. (2016). I also collected these data for all other species in the Feldman et al. (2016) dataset (*N* = 3529) for use in comparisons (Electronic dataset S2.2). Similarly, I gathered information on snake habitats to classify species as either aquatic, arboreal, fossorial, semi-arboreal, or terrestrial. I gathered these data for as many species as I could (*N* = 2646) from field guides and published datasets, including Pizzatto et al. (2007), Lawing et al. (2012), Feldman & Meiri (2014), Bars-Closel et al. (2017), Cyriac & Kodandaramaiah (2018), and Harrington et al. (2018).

I was similarly interested in examining traits of the consumed bird eggs that could provide insight into which bird eggs are at risk of predation by snakes. Because prey bulk (i.e. the cross sectional-diameter of prey) relative to snake size is an important consideration of dietary selectivity in snakes (Greene 1997) I chose to quantify the diameters of consumed eggs. Snakes typically ingest bird eggs length-wise (Gans 1952), and so the diameter of the eggs acts as the main dimensional constraint on ingestion. However, as before, most reports did not include measurements of the dimensions of the eggs consumed. I thus gathered information on average egg diameters for each of the bird species on my list (Electronic dataset S2.1). I gathered these data from resources detailing the reproductive traits of birds that breed in Australia (Garnett et al. 2015), Asia (Tsai et al. 2020), Britain and Europe (Harrison & Castell 2002; Storchová & Hořák 2018), Micronesia (Brandt 1962), North America (Baicich & Harrison 2005), South America (Mason 1985; Auer et al. 2007; Marques-Santos et al. 2015), and southern Africa (Tarboton 2011). For comparative purposes, I also gathered egg diameter data for a geographically and phylogenetically diverse sample of 2326 species of birds (~25% of all birds; Electronic dataset S2.2).

2.3.3 Statistical analyses

I analysed geographical trends of bird egg predation by snakes by comparing the numbers of 1) feeding records, 2) identified snake species and 3) identified bird egg prey species across major geographical regions. I demarcated regions as Africa, Asia, Australia, Central America, Europe, Micronesia, the Middle East, North America, and South America. I also examined the elevation (in metres above sea level) of each area where predation events were observed ($N = 350$). I gathered elevation data for each observation at a resolution of 30 arc seconds from the Worldclim global elevation dataset (Fick & Hijmans 2017).

I evaluated the ecological traits of oophagous snakes by first analysing patterns of their body length distributions. I used a Kolmogorov-Smirnov test to compare the relative distribution of the maximum body lengths of oophagous snakes to all snakes included in Feldman et al. (2016). I then used a phylogenetic ANOVA to test for differences in average log-transformed maximum body lengths of snakes that do and do not consume bird eggs while accounting for the effects of phylogenetic autocorrelation caused by species relatedness. I performed this test with the ‘Geiger’ package (Pennell et al. 2014) in R software v4.1 (R Core Team 2021) across a pruned version of the phylogeny of squamate reptiles published by Tonini et al. (2016) (N = 3503 species) as the input phylogenetic tree. I similarly summarized oophagous snake habitat use and then compared body lengths (log10 transformed) by habitat use controlling for phylogeny via phylogenetic ANOVA.

I tested for the presence of a phylogenetic signal associated with bird egg consumption by snakes by calculating Blomberg's K (Blomberg et al. 2003). I considered a Blomberg's K value less than one to indicate that oophagy occurs randomly across the tree under Brownian motion evolution whereas K values greater than one suggest oophagy is more prevalent between closely related snake taxa (Blomberg et al. 2003). I performed this test using the 'Phytools' package (Revell 2012) in R.

Similar to my analyses of snake body lengths, I performed the same comparative tests between consumed eggs and other eggs. I used a Kolmogorov-Smirnov test to compare the relative distributions of egg diameters of eggs eaten and not eaten by snakes. I then looked for differences in average log-transformed diameters in those groups (N = 2326) via phylogenetic ANOVA. I used a pruned phylogeny of extant birds published by Jetz et al. (2012) as the input tree for this test. Finally, I visually inspected the relationship between bird egg diameters and snake body lengths across all predation events by creating a Sankey plot depicting the flow between egg diameters (in mm) and snake length (in meters). I used bins of 10 mm for bird egg diameters, and bins of 1 m for snake body length size classes.

2.4 Results

2.4.1 Records of bird egg predation by snakes

My search produced a total of 471 records of confirmed predatory interactions between snakes and bird eggs across the globe (Table 2.1). Bird eggs were consumed by 123 different snake taxa (114 species and nine subspecies) belonging to 59 genera and seven families

(Boidae, Colubridae, Elapidae, Psammophiidae, Pseudaspididae, Pythonidae, and Viperidae). Of these, Colubridae (70% of all 123 taxa) and Elapidae (13% of all 123 taxa) were most frequently reported (Fig. 2.1). The eggs of at least 210 species of birds across 159 genera, 71 families and 21 orders, including passerines and several non-passerine orders, were consumed. In 26 cases, bird eggs were only identified to genus, family, or order levels (seven cases, 14 cases, and five cases respectively). In 63 cases, bird eggs were not identified beyond the class level, or the exact identity of the species was ambiguously reported in the source material (for example, “the eggs of land birds”).

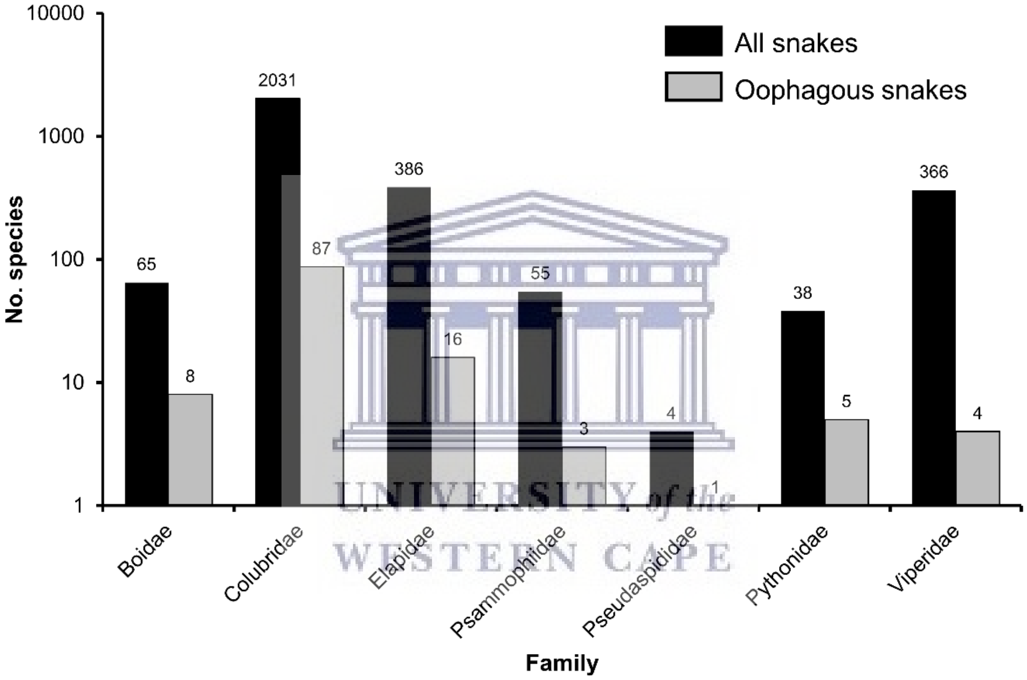

Fig. 2.1: Counts of all species and oophagous species per each snake family with bird egg predators as reported from 471 predation records (*N* = 123 oophagous snake species).

Predation of bird eggs by snakes was reported on all continents on which snakes are distributed as well as on several archipelagos and small islands (Fig. 2.2). The majority of these observations (~75%) occurred at low elevations < 500 m above sea level. Sampling frequencies of feeding records varied between geographical regions (Fig. 2.3) as most predation events were observed in North America (37% of all records) and Africa (24% of all records). At the national level, most records disproportionally represented the relatively well-studied United States of America (35% of all records) and South Africa (14% of all records) respectively. Species richness of snake predators and bird egg prey also both varied regionally and were similarly proportioned to the spread of predation records (Fig. 2.3). Approximately 29% of recorded snake predators were from North America, 20% from Asia, and 17% from Africa. Similarly, 31% of identified bird taxa whose eggs were consumed were from North America, and 23% were from Africa.

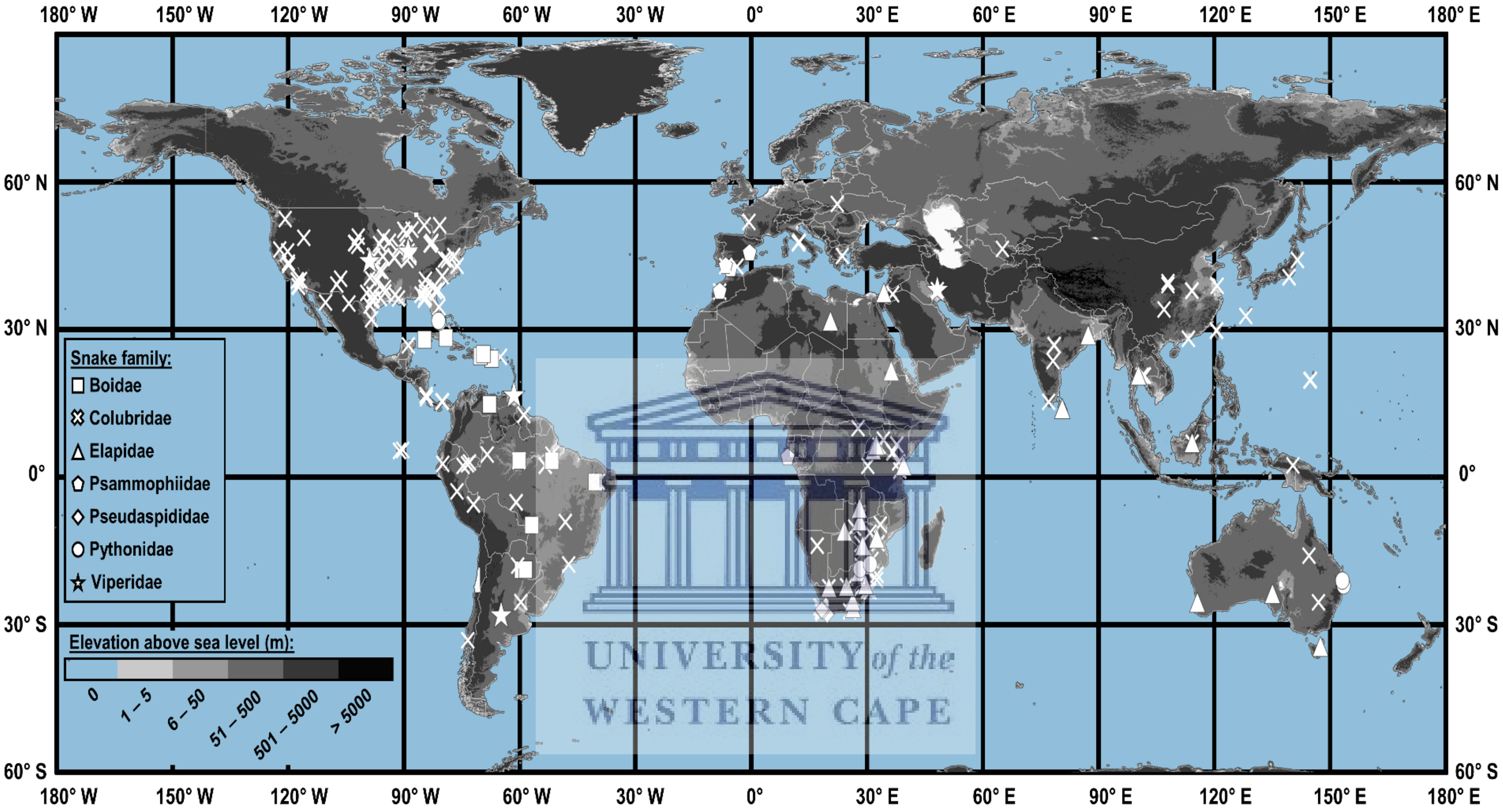

Fig. 2.2: Map of locations of predation events between snakes and bird eggs where coordinates could be determined.

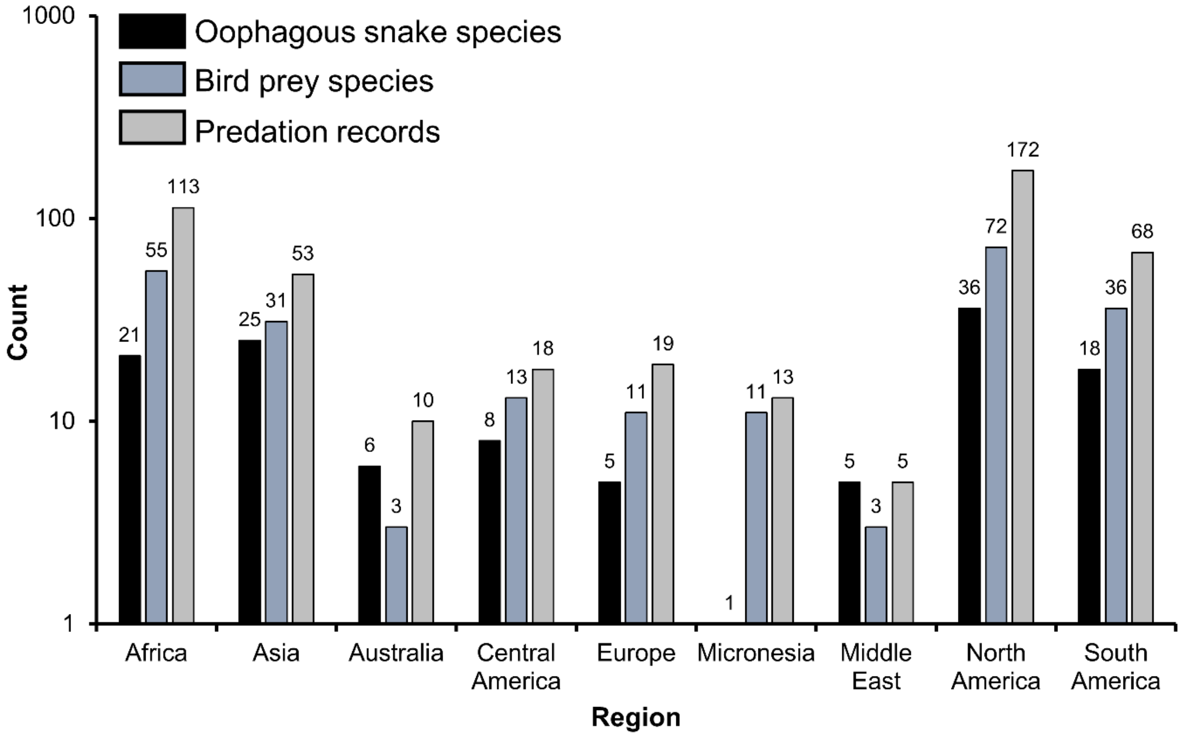

Fig. 2.3: Summary of the numbers of feeding records of snakes eating bird eggs across major continental regions. Values above each bar represent count data.

2.4.2 Which snakes eat bird eggs?

In Africa, the rhombic egg-eater (*Dasypeltis scabra*), was responsible for most reports of egg-eating and was most reported for any snake species (*N* = 53, 11% of all records, Table 2.1). Rhombic egg-eaters consumed the eggs of at least 40 species of birds throughout southern and East Africa, ranging from the southernmost regions of South Africa to Uganda. Other important oophagous African snakes included various species of cobras (*Naja* spp.), boomslang (*Dispholidus typus*), and mole snakes (*Pseudaspis cana*) that were predominantly from southern Africa. Southern and East African pythons (*Python natalensis* and *Python sebae*) were also confirmed as bird egg consumers.

In North America, various rat snakes (*Pantherophis* spp.) were the principal consumers of bird eggs, collectively accounting for 15% of all records (Table 2.1). Other frequently reported species included several species of bullsnakes (*Pituophis* spp.), kingsnakes

(*Lampropeltis* spp.), and eastern racers (*Coluber constrictor*). Collectively, snakes from the above genera consumed the eggs of at least 66 species of bird across the USA (Fig. 2.2). In particular, these snakes were most frequently observed raiding hen-houses for the eggs of domestic chickens (*Gallus gallus domesticus*), and often consumed the eggs of black-capped vireos (*Vireo atricapilla*), field sparrows (*Spizella pusilla*), northern bobwhites (*Colinus virginianus*), and several species of ducks and geese. In Florida, the invasive Burmese python (*Python bivittatus*) consumed the eggs of limpkins (*Aramus guarauna*), American white ibises (*Eudocimus albus*), and introduced helmeted guinea fowl (*Numida meleagris*). Other notable North American oophagous snakes included common garter snakes (*Thamnophis sirtalis*), eastern indigo snakes (*Drymarchon couperi*), and massasaugas (*Sistrurus catenatus*), the only viperid from North America included on my list.

Neotropical snakes from Central and South America that consumed bird eggs mostly included several species of colubrids (Table 2.1). western indigo snakes (*Drymarchon corais*), several species of puffing snakes (*Phrynonax* spp.), and both species of chicken snakes (*Spilotes pullatus* and *S. sulphureus*) were the principal egg predators in these regions. Records involving those species were largely restricted to regions in Brazil and Peru but extended as far south as Chile and as far north as Costa Rica (Fig. 2.2). Collectively, Neotropical colubrids consumed the eggs of at least 20 species of birds. Large boas and anacondas of the genera *Boa*, *Epicrates*, and *Eunectes* were observed consuming the eggs of at least seven species of birds in various habitats in Brazil and Argentina. Similarly, in the Caribbean, several species of Antillean boas (*Chilabothrus* spp.) were notable bird egg predators.

In Europe, only five species of snakes were reported consuming bird eggs (Table 2.1). The most frequently reported species were the four-lined snake (*Elaphe quatuorlineata*) in Italy and the Montpellier snake (*Malpolon monspessulanus*) in Spain. The European adder (*Vipera *berus*) in the United Kingdom, the Aesculapian snake (*Zamenis longissimus*) in Italy and Poland, and the ladder snake (*Zamenis scalaris*) in Spain were also confirmed as oophagous. Those snakes were frequently recorded consuming the eggs of common pheasants (*Phasianus colchicus*), great tits (*Parus major*), common linnets (*Linaria cannabina*), and common babblers (*Argya caudata*). I only found one record of bird egg predation in the Middle East which was of the Arabian tiger snake (*Telescopus dhara*).

Across the oceanic region of Asia, Australia, and Micronesia, cat snakes of the genus *Boiga* were the predominant bird egg predators. Records of these snakes accounted for 6% of the dataset (Table 2.1). More than half of those observations were of the invasive brown tree snake (*Boiga irregularis; N* = 16) on the island of Guam (Fig. 2.2). Predations by other cat snakes (*B. cyanea*, *B. cynodon*, *B. dendrophilia*, *B. kraepelini*, *B. ochracea*, and *B. siamensis*) were observed on several islands and coastal regions of South-East Asia. Asian rat snakes (*Elaphe* spp.) were important predators of bird eggs in habitats across China and offshore Japan. In India and surrounding areas, the bird egg specialist Indian egg-eater (*Boiga westermanni*) purportedly consumed the eggs of several species of birds similarly to African *Dasypeltis*. However, few feeding records for these snakes have been published. Lastly, while few observations were reported from Australia, at least two species of pythons (*Liasus fuscus* and *Morelia spilota*) and three species of elapid snakes (*Denisonia devisi*, *Notechis scutatus*, and *Pseudechis australis*) consumed bird eggs in this region.

Table 2.1: Recorded observations of avian oophagy by snakes.

Snake species	Snake common name	Bird species (no. recorded)	Bird common name	Geographic area	Source
Boidae					
Boa constrictor	Boa constrictor	*Butorides striatus*	Striated heron	Venezuela	Thomas (1984)
		Ciconia maguari	Maguari stork	Venezuela	Thomas (1984)
		Forpus passerinus	Green-rumped parrotlet	Venezuela	Menezes & Marini (2017)
		Phimosus infuscatus	Bare-faced ibis	Venezuela	Thomas (1984)
Chilabothrus angulifer	Cuban boa	*Patagioenas leucocephala*	White-crowned pigeon	Cuba	Godínez et al. (1987)
		Petrochelidon fulva	Cave swallow	Cuba	Mancina & Sosa (1997)
Chilabothrus chrysogaster	Turk's Island boa	*Gallus domesticus*[‡] (2)	Domestic chicken	West Indies	Schwartz & Henderson (1991)
Chilabothrus inornatus	Puerto Rican boa	*Bubulcus ibis*	Cattle egret	Puerto Rico	Wiley (2003)
		Gallus gallus domesticus[‡]	Domestic chicken	Jamaica	Gosse (1851)
Chilabothrus striatus	Hispaniolan boa	*Phasianus colchicus*	Ring-necked pheasant	Dominican Republic	Ottenwalder (1980)
		Ploceus cucullatus	Village weaver	Dominican Republic	Wiley (2001)
		Psittacara chloropterus	Hispaniolan parakeet	Dominican Republic	Ottenwalder (1980)
Epicrates assisi	Striped rainbow boa	Unidentified	-	Brazil	Vitt & Vanglider (1983)
Epicrates cenchria	Rainbow boa	*Conopophaga peruviana*	Ash-throated gnateater	Peru	Londoño pers comm.
		Tinamus tao	Grey tinamou	Brazil	Fiorillo (2019)
		Unidentified	-	Brazil	Martins & Oliveira (1998)
Eunectes notaeus	Yellow anaconda	*Aramus guarauna* (3)	Limpkin	Argentina; Brazil	Strüssmann & Sazima (1991); Waller et al. (2007); Miranda et al. (2017)
		Chauna torquata (2)	Southern screamer	Argentina	Waller et al. (2007); Miranda et al. (2017)
Colubridae					
Boiga cyanea	Green cat snake	*Malacopteron cinereum*	Scaly-crowned babbler	Thailand	Somsiri et al. (2019)

		Unidentified	-	Thailand	Pierce & Pobprasert (2013)
Boiga cynodont	Dog-toothed cat snake	Unidentified	-	South-East Asia	Greene (1989)
Boiga dendrophila	Mangrove cat snake	*Gallus gallus domesticus*[‡]	Domestic chicken	Borneo	Pitman (1962b)
		Unknown "sea birds"	-	Borneo	Pitman (1962b)
Boiga irregularis	Brown tree snake	*Anas platyrhynchos*[‡]	Mallard	Guam	Savidge (1988)
		Columba livia	Rock pigeon	Guam	Savidge (1988)
		Coturnix coturnix[‡]	Common quail	Guam	Savidge (1988)
		Francolinus francolinus	Black francolin	Guam	Vice et al. (2005)
		Gallus gallus	Red junglefowl	Guam	Savidge (1988)
		Melopsittacus undulatus[‡]	Budgerigar	Guam	Savidge (1988)
		Nymphicus hollandicuss[‡]	Cockatiel	Guam	Savidge (1988)
		Passer montanus	Eurasian tree sparrow	Guam	Savidge (1988)
		Serinus canarius[‡]	Island canary	Guam	Savidge (1988)
		Streptopelia bitorquata (2)	Sunda collared dove	Guam	Conry (1988); Savidge (1988)
		Taeniopygia guttata	Sunda zebra finch	Guam	Savidge (1988)
		Unidentified (4)	-	Australia; Guam	Savidge (1988); Greene (1989); Shine (1991a)
Boiga kraepelini	Kelung cat snake	*Alcippe morrisonia*	Grey-cheeked fulvetta	Taiwan	Chen et al. (2015)
		Pitta nympha	Fairy pitta	Taiwan	Chen et al. (2015)
		Pomatorhinus musicus	Taiwan scimitar babbler	Taiwan	Chen et al. (2015)
		Pycnonotus sinensis	Light-vented bulbul	Taiwan	Chen et al. (2015)
		Schoeniparus brunneus	Dusky fulvetta	Taiwan	Chen et al. (2015)
		Unidentified	-	East Asia	Greene (1989)
Boiga ochracea	Tawny cat snake	Unidentified	-	N/a	Greene (1989)
Boiga siamensis	Gray cat snake	Unidentified	-	South-East Asia	Greene (1989)
Borikenophis portoricensis	Puerto Rican racer	*Zenaida aurita*	Zenaida dove	Virgin Islands	Norton (1993)
Chironius grandisquamis	Ecuador sipo	*Poliocrania exsul*	Chestnut-backed antbird	Costa Rica	Visco & Sherry (2015)
Clelia clelia	Black mussurana	*Myrmoborus leucophrys*	White-browed antbird	Peru	Londoño pers comm.
Coluber constrictor constrictor	Northern black racer	*Colinus virginianus* (2)	Northern bobwhite	USA	Uhler et al. (1939); Staller et al. (2005)

		Haematopus palliatus	American oystercatcher	USA	Hackney et al. (2014)
		Passerina cyanea	Indigo bunting	USA	Stake et al. (2005)
		Spizella pusilla	Field sparrow	USA	Best (1974)
		Turdus migratorius (2)	American robin	USA	Fitch (1963b); Rodirguez-Robles & de Jesus-Escobar (1999)
		Vireo atricapilla	Black-capped vireo	USA	DeGregorio et al. (2016a)
Coluber constrictor flaviventris	Yellowbelly racer	*Agelaius phoeniceus*	Red-winged blackbird	USA	Fitch (1963b)
		Cardinalis cardinalis	Northern cardinal	USA	Fitch (1963b)
Coluber constrictor foxii	Blue racer	*Sialia sialis*	Eastern bluebird	USA	Lennon (2013)
Conophis lineatus	Road guarder	*Morococcyx erythropygus*	Lesser ground-cuckoo	Costa Rica	Scott (1983)
Dasypeltis atra	Montane egg-eater	*Phyllastrephus cabanisi*	Cabanis's greenbul	Kenya	Van de Loock & Bates (2016)
		Unknown weaver	-	Uganda	Pitman (1974)
Dasypeltis inornata	Southern brown egg-eater	*Gallus gallus domesticus*[‡]	Domestic chicken	South Africa	Maritz & Ping (2020)[†]
Dasypeltis medici	East African egg-eater	*Phyllastrephus flavostriatus*	Yellow-streaked greenbul	Mozambique	Macdonald & Dean (1978)
Dasypeltis scabra	Rhombic egg-eater	*Anthus cinnamomeus*	African pipit	South Africa	Bates & Little (2013)
		Cercotrichas coryphaeus	Karoo scrub-robin	South Africa	Lloyd et al. (2009)
		Columba guinea (2)	Speckled pigeon	South Africa	Dyer (1996)
		Coturnix coturnix	Common quail	South Africa	Bates & Little (2013)
		Crithagra flaviventris	Yellow canary	South Africa	Hockey et al. (2005)
		Euplectes ardens	Red-collared widowbird	South Africa	Pryke & Lawes (2004)
		Euplectes orix	Southern red bishop	South Africa	Kok et al. (1977)
		Gallus gallus domesticus[‡] (3)	Domestic chicken	South Africa; Uganda	Loveridge (1936); Pitman (1958b); Maritz & Maritz (2020)
		Haematopus moquini (2)	African oystercatcher	South Africa	Bates & Little (2013); Maritz & Maritz (2020)
		Lagonosticta nitidula	Brown firefinch	South Africa	Hockey et al. (2005)

Lanius collaris	Southern fiscal	South Africa	Bruderer (1991)
Larus dominicanus	Kelp gull	South Africa	Dyer (1996)
Larus hartlaubii	Hartlaub's gull	South Africa	Underhill et al. (2009)
Macronyx capensis	Cape longclaw	South Africa	Bates & Little (2013)
Malcorus pectoralis	Rufous-eared warbler	South Africa	Hockey et al. (2005)
Melaenornis infuscatus	Chat flycatcher	South Africa	Lloyd (2004)
Merops sp.	-	South Africa	Fry (1984)
Passer melanurus	Cape sparrow	South Africa	Underhill et al. (2009)
Pavo cristatus[‡] (3)	Indian peafowl	South Africa; Zimbabwe	Olivier (2020)[†]; Schick (2019)[†]
Phalacrocorax capensis	Cape cormorant	South Africa	Dyer (1996)
Phalacrocorax coronatus	Crowned cormorant	South Africa	Underhill et al. (2009)
Philetairus socius	Sociable weaver	South Africa	Hockey et al. (2005)
Ploceus castanops	Northern brown-throated weaver	Uganda	Pitman (1958b)
Ploceus cucullatus	Village weaver	Uganda	Pitman (1958b)
Ploceus nigerimus	Vieillot's black weaver	Uganda	Pitman (1958b)
Ploceus sp.	-	South Sudan	Pitman (1962a)
Poicephalus rueppellii	Rüppell's parrot	Namibia	Selman (1998)
Prinia flavicans	Black-chested prinia	South Africa	Jacobsen (1989)
Prinia maculosa (2)	Karoo prinia	South Africa	Rowan & Bruekhusen (1962); Nalwanga et al. (2004)
Pseudonigrita arnaudi	Grey-capped social weaver	Kenya	Cheng et al. (2019)
Pterocles namaqua	Namaqua sandgrouse	South Africa	Lloyd et al. (2001)
Pycnonotus capensis (2)	Cape bulbul	South Africa	Kruger (2004); Hockey et al. (2005)
Quelea quelea lathami	Red-billed quelea	South Africa	Pienaar (1969)
Sarothrura boehmi	Streaky-breasted flufftail	Zambia	Jamie et al. (2016)

		Scleroptila africanus	Grey-winged francolin	South Africa	Little & Crowe (1993)
		Spermestes cucullatus	Bronze mannikin	Kenya	Loveridge (1945)
		Sporaeginthus subflavus	Orange-breasted waxbill	South Africa	Colahan (1982)
		Sterna bergii	Greater crested tern	South Africa	Underhill et al. (2009)
		Streptopelia senegalensis	Laughing dove	South Africa	Rowan (1983)
		Threskiornis aethiopicus	African sacred ibis	South Africa	Underhill et al. (2009)
		Unknown weaver	-	South Africa	Barbour & Loveridge (1928)
		Vanellus lugubris	Senegal lapwing	South Africa	Ward (1989)
		Unidentified (3)	-	DRC; Mozambique; South Africa	Schmidt et al. 1923; Loveridge (1953); De Waal (1977)
Dendrelaphis tristis	Daudin's bronzeback snake	*Copsychus fulicatus*	Indian robin	Sri-Lanka	Pitman (1962b)
Dendrophidion percarinatum	South American forest racer	*Poliocrania exsul*	Chestnut-backed antbird	Costa Rica	Visco & Sherry (2015)
Dispholidus typus	Boomslang	*Philetairus socius*	Sociable weaver	South Africa	Greuel (2020)
		Poicephalus rueppellii	Rüppell's parrot	Namibia	Selman et al. (2000)
		Prinia maculosa	Karoo prinia	South Africa	Nalwanga et al. (2004)
		Rhinopomastus cyanomelas	Common scimitarbill	Zimbabwe	Pitman (1962a)
		Serinus canicollis	Cape canary	South Africa	Pitman (1962a)
		Spermestes cucullatus	Bronze mannikin	Kenya	Loveridge (1945)
		Unknown weaver	-	South Africa	Pitman (1958a)
		Unidentified (3)	-	South Africa; Sudan; Tanzania	Barbour & Loveridge (1928); Smith et al. (2019); Maritz & Maritz (2020)
Drymarchon corais	Western indigo snake	*Gallus gallus domesticus*‡	Domestic chicken	Brazil	Bernarde & Abe (2006)
		Unknown phasianid (3)	-	Brazil	da Costa-Prudente et al. (2014)
		Unidentified (2)	-	Brazil	Bernarde & Abe (2006); Menezes & Marini (2017)

Drymarchon couperi	Eastern indigo snake	*Gallus gallus domesticus*‡ (2)	Domestic chicken	USA	Stevenson et al. (2010); Campbell & Smith (2018)†
Drymarchon melanurus	Blacktail cribo	*Ortalis vetula mccalli*	Plain chachalaca	USA	Marion & Fleetwood (1978)
Dryocalamus sp.		*Malacopteron cinereum*	Scaly-crowned babbler	Thailand	Somsiri et al. (2019)
Boiga westermanni	Indian egg-eater	*Columba livia*	Rock pigeon	India	Visvanthan (2015)
		Passer domesticus	House sparrow	India	Dandge (2008)
		Ploceus philippinus	Baya weaver	India	Dandge & Tiple (2016)
		Unidentified	-	India	Dandge (2008)
Elaphe anomala	Korean rat snake	*Paradoxornis heudei*	Reed parrotbill	China	Chen et al. (2020)
Elaphe carinata	Taiwanese rat Snake	*Accipter soloensis*	Chinese sparrowhawk	China	Ma et al. (2016)
		Aegithalos glaucogularis	Silver-throated bushtit	China	Li et al. (2012)
		Chrysolophus pictus	Golden pheasant	China	Wang et al. (2014)
		Nipponia nippon (2)	Crested ibis	China	Yu et al. (2006); Yu et al. (2015)
		Pomatorhinus musicus	Taiwan scimitar babbler	China; Taiwan	Chen et al. (2015)
Elaphe climacophora	Japanese rat snake	Unidentified	-	Japan	Mori & Nagata (2016)
Elaphe quadrivirgata	Japanese four-lined rat snake	Unknown "land birds"	-	Japan	Hasegawa & Moriguchi (1989)
		Unknown "sea birds"	-	Japan	Hasegawa & Moriguchi (1989)
Elaphe quatuorlineata	Four-lined rat snake	*Dendrocopos major*	Great spotted woodpecker	Italy	Cattaneo (1979)
		Parus major	Great tit	Italy	Sorace et al. (2000)
		Passer domesticus	House sparrow	Italy	Cattaneo (1979)
		Phasianus colchicus (2)	Ring-necked pheasant	Greece; Italy	Cattaneo (1979); Cattaneo & Grano (2013)
		Unidentified (2)	-	Italy	Filipi et al. (2005)
Elaphe schrenkii	Amur rat snake	Unidentified	-	China	Schultz (1988)
Elaphe taeniura	Beauty snake	*Accipter soloensis*	Chinese sparrowhawk	China	Ma et al. (2016)
		Aegithalos concinnus	Black-throated bushtit	China	Li et al. (2012)
		Collocalia sp.	-	Borneo	Pitman (1962b)
		Emberiza jankowskii	Jankowski's bunting	China	Jiang et al. (2008)

Elaphe taeniura friesi	Taiwanese beauty snake	*Pitta nympha*	Fairy pitta	Taiwan	Chen et al. (2015)
Hemorrhois hippocrepis	Horseshoe whip snake	*Pterocles orientalis*	Black-bellied sandgrouse	Morocco	Znari et al. (2008)
Heterodon nasicus	Western hognose snake	*Chondestes grammacus*	Lark sparrow	USA	Langford & Janovy (2011)
Lampropeltis alterna	Grey-banded kingsnake	*Callipepla squamata*	Scaled quail	USA	Vermilya & Acuna (2004)
Lampropeltis californiae	California kingsnake	*Aimophila ruficeps*	Rufous-crowned sparrow	USA	Morrison & Bolger (2002)
		Callipepla californica (3)	California quail	Mexico; USA	Klauber (1931); Compton (1933); Wisemen et al. (2019)
		Vireo bellii	Bell's vireo	USA	Pemberton & Carriger (1916)
		Zenaida macroura	Mourning dove	USA	Hollingsworth (2016)
Lampropeltis calligaster	Prairie kingsnake	*Colinus virginianus* (2)	Northern bobwhite	USA	Fitch (1978); Fitch (1998)
		Coturnix coturnix	Common quail	USA	Klimstra (1959)
		Passerina cyanea	Indigo bunting	USA	Thompson et al. (1999)
		Spizella pusilla	Field sparrow	USA	Thompson et al. (1999)
Lampropeltis getula	Common kingsnake	*Colinus virginianus*	Northern bobwhite	USA	Staller et al. (2005)
		Molothrus ater	Brown-headed cowbird	USA	Cavitt (2000)
		Spiza americana	Dickcissel	USA	Cavitt (2000)
		Unknown passerine	-	USA	Cavitt (2000)
		Unidentified	-	USA	Rodriguez-Robles & de Jesus-Escobar (1999)
Lampropeltis holbrooki	Speckled kingsnake	*Passerina cyanea*	Indigo bunting	USA	Stake et al. (2005)
		Spizella pusilla	Field sparrow	USA	Stake et al. (2005)
		Sturnella magna	Eastern meadowlark	USA	Landoll & Husak (2011)
Lampropeltis triangulum	Eastern milksnake	*Melospiza melodia*	Song sparrow	USA	Brown (1979b)
		Spizella pusilla	Field sparrow	USA	Bent & Austin Jr (1968)
Lampropeltis zonata	California mountain kingsnake	*Oreortyx pictus*	Mountain quail	USA	Wentz (1953)

		Unidentified	-	USA	Rodriguez-Robles & de Jesus-Escobar (1999)
Leptophis ahaetulla	Giant parrot snake	Unidentified	-	Argentina	Lopez et al. (2003)
Leptophis mexicanus	Mexican parrot snake	Unidentified	-	Mexico	Henderson (1982)
Lycodon davisonii	Blanford's bridle snake	*Alophoixus pallidus*	Puff-throated bulbul	Thailand	Khamcha & Gale (2020)
		Cyornis sumatrensis	Indochinese blue flycatcher	Thailand	Khamcha & Gale (2020)
		Kittacincla malabarica	White-rumped shama	Thailand	Khamcha & Gale (2020)
		Malacocincla abbotti	Abbott's babbler	Thailand	Khamcha & Gale (2020)
		Malacopteron cinereum	Scaly-crowned babbler	Thailand	Khamcha & Gale (2020)
		Pycnonotus finlaysoni	Stripe-throated bulbul	Thailand	Khamcha & Gale (2020)
Lycodon semicarinatus	Ryukyu odd-tooth snake	*Otus elegans*	Ryukyu scops owl	Japan	Toyama et al. (2015)
Masticophis bilineatus	Sonoran whipsnake	*Zenaida asiatica*	White-winged dove	Mexico	Gatica-Colima (2015)
Masticophis flagellum	Coachwhip	*Vireo atricapilla*	Black-capped vireo	USA	Stake & Cimprich (2003)
Oligodon formosanus	Formosa kukri snake	*Pomatorhinus musicus*	Taiwan scimitar babbler	Taiwan	Chen et al. (2015)
Opheodrys aestivus	Rough greensnake	*Vireo atricapilla*	Black-capped vireo	USA	Nelson et al. (2006)
Oxyrhopus petola	Forest flame snake	*Conopophaga ardesiaca*	Slaty gnateater	Peru	Londoño pers comm.
		Hafferia fortis	Sooty sntbird	Peru	Cerón-Cardona & Londoño (2017)
		Unidentified (2)	-	Brazil	Cunha & Nascimento (1983); Gaiarsa et al. (2013)
Pantherophis alleghaniensis	Eastern rat snake	*Gallus gallus domesticus*[‡] (4)	Domestic chicken	USA	Brown & Mitchell (2005); Folsom 2018; Jokay 2020; Rice 2020
		Picoides borealis	Red-cockaded woodpecker	USA	Delaney et al. (2008)
		Vireo atricapilla	Black-capped vireo	USA	DeGregorio et al. (2016a)

Pantherophis emoryi	Great Plains rat snake	*Bartramia longicauda*	Upland sandpiper	USA	Cavitt (2000)
		Setophaga chrysoparia (2)	Golden-cheeked warbler	USA	Stake (2001); Stake et al. (2004)
Pantherophis guttatus	Eastern corn snake	*Colinus virginianus*	Northern bobwhite	USA	Staller et al. (2005)
		Setophaga chrysoparia	Golden-cheeked warbler	USA	Stake et al. (2005)
		Vireo atricapilla	Black-capped vireo	USA	Stake et al. (2005); DeGregorio et al. (2016b)
		Unidentified	-	USA	Rodriguez-Robles & de Jesus-Escobar (1999)
Pantherophis obsoletus	Western rat snake	*Aix sponsa* (2)	Wood duck	USA	Leopold (1966); Hansen & Frederickson (1990)
		Anas platyrhynchos‡	Mallard	USA	Ormand (2019)†
		Aphelocoma coerulescens	Florida scrub-jay	USA	Carter et al. (2007)
		Bonasa umbellus	Ruffed grouse	USA	Brown (1979a)
		Branta canadensis maxima	Canada goose	USA	Aldrich & Endicott (1984)
		Colinus virginianus (2)	Northern bobwhite	USA	Uhler et al. (1939); Staller et al. (2005)
		Coturnix coturnix	Common quail	USA	Conant (1938)
		Dendrocygna autumnalis	Black-bellied whistling-duck	USA	Schramer (2019)†
		Egretta caerulea	Little blue heron	USA	Taylor & Michael (1971)
		Gallus gallus domesticus‡ (10)	Domestic chicken	USA	Brown (1979a); Stickel et al. (1980); Smith (2017)†; Brown & Smith (2017)†; Allison & Smith (2018)†; Shellabarger (2019)†; Ormand (2019)†; Calhoun (2020)†; Wilkerson

					(2020)†; Hayes & Rice (2020)†
		Hirundo rustica	Barn swallow	USA	Carter (1970)
		Passer domesticus	House sparrow	USA	Wishard & Cavataio (2020)†
		Passerina cyanea (2)	Indigo bunting	USA	Thompson et al. (1999); Stake et al. (2005)
		Setophaga chrysoparia (2)	Golden-cheeked warbler	USA	Stake et al. (2004); Stake et al. (2005)
		Sialia sialis	Eastern bluebird	USA	Brown (1979a)
		Spizella pusilla (2)	Field sparrow	USA	Thompson et al. (1999); Stake et al. (2005)
		Thryothorus ludovicianus	Carolina wren	USA	Brown (1979a)
		Turdus sp.	-	USA	Britto (2020)†
		Unknown duck	-	USA	Stickel et al. (1980)
		Vireo atricapilla	Black-capped vireo	USA	Stake et al. (2005)
		Zenaida macroura	Mourning dove	USA	Fitch (1963a)
		Unidentified (3)	-	USA	Fitch (1963a); Stickel et al. (1980); Rodriquez-Robles & de Jesus-Escobar (1999)
Pantherophis spiloides	Midland rat snake	*Bubulcus ibis*	Cattle egret	USA	Dusi & Dusi (1968)
		Egretta caerulea	Little blue heron	USA	Dusi & Dusi (1968)
Pantherophis vulpinus	Eastern fox snake	*Anas clypeata*	Northern shoveler	USA	Wheeler (1984)
		Anas discors	Blue-winged teal	USA	Andrews (1952)
		Anas discors	Blue-winged teal	USA	Wheeler (1984)
		Anas platyrhynchos	Mallard	USA	Andrews (1952)
		Coturnix coturnix	Common quail	USA	Conant (1938)
		Gallus gallus domesticus‡ (2)	Domestic chicken	USA	Conant (1938); Jadin & Orlofske (2020)
		Melospiza melodia	Song sparrow	USA	Langlois (1964)

		Mergus merganser	Common merganser	Canada	Wilson (1985)
		Phasianus colchicus (3)	Ring-necked pheasant	Canada; USA	Stokes (1952); Langlois (1964); Vogt (1981)
		Spiza americana	Dickcissel	USA	Klug et al. (2010)
		Unknown duck	-	Canada	Rivard (1976)
		Unidentified	-	USA	Rodriguez-Robles & de Jesus-Escobar (1999)
Philodryas patagoniensis	Patagonia green racer	*Xanthopsar flavus*	Saffron-cowled blackbird	Argentina	Fraga et al. (1998)
Philothamnus hoplogaster	Green water snake	*Streptopelia capicola*	Ring-necked dove	Zimbabwe	Pitman (1962b)
Phrynonax poecilonotus	Puffing snake	*Aramides cajanea*	Gray-cowled wood-rail	Panama	Robinson & Robinson (2001)
		Crotophaga major	Greater ani	Panama	Riehl & Jara (2009)
		Hafferia fortis	Sooty antbird	Peru	Cerón-Cardona & Londoño (2017)
		Hylophylax naevioides	Spotted antbird	Panama	Robinson et al. (2005)
		Penelope jacquacu	Spix's guan	Peru	Dixon & Soini (1986)
		Penelope sp.	-	Brazil	Martins & Oliveira (1998)
		Poliocrania exsul (2)	Chestnut-backed antbird	Costa Rica; Panama	Robinson et al. (2005); Visco & Sherry (2015)
		Tinamus major	Great tinamou	Panama	Robinson & Robinson (2001)
		Unknown seedeater	-	Guyana	Beebe (1946)
		Unidentified (2)	-	Chile; Panama	Sexton & Heatwole (1965), Menezes & Marini (2017)
Phrynonax polylepis	Northeastern puffing snake	*Ortalis guttata*	Speckled chachalaca	Peru	Angulo & Chavez (2017)
		Penelope jacquacu (2)	Spix's guan	Peru	Dixon & Soini (1986)
		Sporophila sp.	-	Guyana	Beebe (1946)
Phrynonax shropshirei	Shropshire's puffing snake	Unidentified	-	Ecuador	Cisneros-Heredia (2005)
Pituophis catenifer	Gopher snake	*Anas acuta*	Northern pintail	USA	Rodriguez-Robles (2002)

Anas platyrhynchos	Mallard	USA	Rodriguez-Robles (2002)
Aythya americana	Redhead	USA	Rodriguez-Robles (2002)
Callipepla californica	California quail	USA	Rodriguez-Robles (2002)
Callipepla gambelii	Gambel's quail	USA	Rodriguez-Robles (2002)
Colinus virginianus	Northern bobwhite	USA	Cavitt (2000)
Coturnix coturnix	Common quail	USA	Rodriguez-Robles (2002)
Eremophila alpestris	Horned lark	USA	Rodriguez-Robles (2002)
Gallus gallus domesticus[‡]	Domestic chicken	USA	Rodriguez-Robles (2002)
Lanius ludovicianus	Loggerhead shrike	USA	Hathcock (2013)
Melanerpes formicivorus	Acorn woodpecker	USA	Rodriguez-Robles (2002)
Numenius americanus	Long-billed curlew	USA	Rodriguez-Robles (2002)
Numida meleagris	Helmeted guineafowl	USA	Rodriguez-Robles (2002)
Otus flammeolus	Flammulated owl	USA	Rodriguez-Robles (2002)
Pheucticus melanocephalus	Black-headed grosbeak	USA	Pemberton & Carriger (1916)
Quiscalus quiscula	Common grackle	USA	Rodriguez-Robles (2002)
Recurvirostra americana	American avocet	USA	Rodriguez-Robles (2002)
Sialia currucoides	Mountain bluebird	USA	Rodriguez-Robles (2002)
Sialia mexicana	Western bluebird	USA	Rodriguez-Robles (2002)
Spiza americana	Dickcissel	USA	Rodriguez-Robles (2002)
Stelgidopteryx serripennis	Northern rough-winged swallow	USA	Rodriguez-Robles (2002)
Sturnella sp.	-	USA	Rodriguez-Robles (2002)
Troglodytes aedon	House wren	USA	Rodriguez-Robles (2002)
Turdus migratorius	American robin	USA	Rodriguez-Robles (2002)

		Unknown duck	-	USA	Rodriguez-Robles (2002)
		Unknown passerine	-	USA	Rodriguez-Robles (2002); Weaver (2004)
		Zenaida macroura	Mourning dove	USA	Rodriguez-Robles (2002)
		Unidentified	-	USA	Rodriguez-Robles (2002)
Pituophis catenifer affinis	Sonoran gopher snake	*Coccyzus americanus*	Yellow-billed cuckoo	USA	Root et al. (2015)
Pituophis catenifer deserticola	Great Basin gopher snake	*Centrocercus urophasianus*	Greater sage-grouse	USA	Lockyer et al. (2013)
Pituophis catenifer sayi	Bullsnake	*Anas platyrhynchos*	Mallard	USA	USFW & Smith (2018)[†]
		Aythya americana	Redhead	USA	Imler (1945)
		Cistothorus palustris	Marsh wren	USA	Imler (1945)
		Colinus virginianus	Northern bobwhite	USA	Brown (1979a)
		Fulica americana	American coot	USA	Imler (1945)
		Mareca strepera	Gadwall	USA	Imler (1945)
		Meleagris gallopavo	Wild turkey	USA	Guthrie (1932)
		Phasianus colchicus	Ring-necked pheasant	USA	Imler (1945)
		Recurvirostra americana (2)	American avocet	USA	Imler (1945)
		Stelgidopteryx ruficollis	Southern rough-winged swallow	USA	Best (1977)
		Sturnella magna	Eastern meadowlark	USA	Imler (1945)
		Turdus merula	Eurasian blackbird	USA	Imler (1945)
		Unknown duck	-	USA	Imler (1945)
		Unidentified (2)	-	USA	Diller & Wallace (1996); Iverson & Akre (2001)
Pituophis melanoleucus lodingi	Black pine snake	*Colinus virginianus*	Northern bobwhite	USA	Rudolph et al. (2002)
Pituophis melanoleucus melanoleucus	Northern pine snake	*Aix sponsa*	Wood duck	USA	Wheeler (1984)
		Colinus virginianus	Northern bobwhite	USA	Brown (1979a)
Platyceps rhodorachis	Common cliff racer	*Argya caudata*	Common babbler	Iran	Moosavi et al. (2011)
Pseudalsophis dorsalis	Central Galapagos racer	*Zenaida galapagoensis*	Galapagos dove	Ecuador	Ortiz-Catedral et al. (2019)
		Unidentified	-	Ecuador	Ortiz-Catedral et al. (2019)

Pseudalsophis occidentalis	Western Galapagos racer	Unidentified	-	Ecuador	Ortiz-Catedral et al. (2019)
Ptyas dhumnades	Big-eyed rat snake	*Accipter soloensis*	Chinese sparrowhawk	China	Ma et al. (2016)
		Aegithalos concinnus	Black-throated bushtit	China	Li et al. (2012)
Ptyas mucosus	Oriental rat snake	*Hypsipetes ganeesa*	Square-tailed bulbul	India	Balakrishnan (2010)
		Pitta nympha	Fairy pitta	Taiwan	Chen et al. (2015)
Rhachidelus brazili	Brazilian bird snake	Unidentified (2)	-	Brazil	França et al. (2008); Gaiarsa et al. (2013)
Spalerosophis diadema	Diadem snake	*Podoces panderi*	Turkestan ground jay	Uzbekistan	Burnside et al. (2020)
Spilotes pullatus	Tropical chicken snake	*Crotophaga major*	Greater ani	Panama	Riehl & Jara (2009)
		Turdus rufiventris	Rufous-bellied thrush	Brazil	Cochran (2013)
		Turdus sp.	-	Brazil	Marques & Sazima (2004)
		Unidentified (2)	-	Brazil	Martins & Oliveira (1998); Menezes & Marini (2017)
Spilotes sulphureus	Yellow-bellied chicken snake	*Campylopterus largipennis*	Grey-breasted sabrewing	Peru	Londoño pers comm.
		Chlorothraupis carmioli	Carmiol's tanager	Peru	Londoño pers comm.
		Conopophaga peruviana	Ash-throated gnateater	Peru	Londoño pers comm.
		Cryptopipo holochlora	Green manakin	Peru	Londoño pers comm.
		Crypturellus bartletti	Bartlett's tinamou	Peru	Londoño pers comm.
		Crypturellus variegatus	Variegated tinamou	Peru	Londoño pers comm.
		Dysithamnus mentalis	Plain antvireo	Peru	Londoño pers comm.
		Geotrygon montana	Ruddy quail-dove	Peru	Londoño pers comm.
		Glyphorynchus spirurus	Wedge-billed woodcreeper	Peru	Londoño pers comm.
		Hylophylax naevius	Spot-backed antbird	Peru	Londoño pers comm.
		Lepidothrix coronata	Blue-crowned manakin	Peru	Londoño pers comm.

		Myrmoborus myotherinus	Black-faced antbird	Peru	Londoño pers comm.
		Myrmothera campanisona	Thrush-like antpitta	Peru	Londoño pers comm.
		Saltator maximus	Buff-throated saltator	Peru	Londoño pers comm.
		Sclerurus mexicanus	Tawny-throated leaftosser	Peru	Londoño pers comm.
		Tangara schrankii	Green-and-gold tanager	Peru	Londoño pers comm.
		Tinamus major	Great tinamou	Peru	Londoño pers comm.
		Unknown passerine	-	Brazil	Londoño pers comm.
		Willisornis poecilinotus	Common scale-backed antbird	Peru	Londoño pers comm.
		Unidentified	-	Peru	dos Santos-Costa et al. (2015)
Telescopus dhara	Arabian tiger snake	Unknown passerine	-	Jordan	Amr & Disi (1998)
Thamnophis hammondii	Two-striped garter snake	*Spizella atrogularis*	Black-chinned sparrow	USA	Pemberton & Carriger (1916)
Thamnophis sirtalis	Common garter snake	*Dolichonyx oryzivorus*	Bobolink	USA	Gabrielson (1922)
		Spiza americana	Dickcissel	USA	Olson & Warner (2001)
		Spizella pusilla	Field sparrow	USA	Olson & Warner (2001)
Toxicodryas blandingii	Blandings tree snake	Unidentified (2)	-	Uganda	Cansdale (1961); Pitman (1974)
Zamenis longissimus	Aesculapian snake	*Muscicapa striata*	Spotted flycatcher	Poland	Najbar (2007)
		Unidentified (2)	-	Italy	Naulleau & Bonnet (1995); Capula & Luiselli (2002)
Zamenis scalaris	Ladder snake	*Burhinus oedicnemus*	Eurasian stone-curlew	Spain	Solis & De Lope (1995)
		Unidentified	-	Spain	Pleguezuelos et al. (2007)
Elapidae					
Bungarus fasciatus	Banded krait	*Gallus gallus*	Red junglefowl	India	Slowinski (1994)
Denisonia devisi	De Vis's banded snake	*Chrysococcyx basalis*	Horsfield's bronze cuckoo	Australia	Linton (1930)
Laticauda colubrina	Yellow-lipped sea krait	*Sterna sumatrana*	Black-naped tern	Borneo	Pitman (1962a)

Naja anchietae	Anchieta's cobra	*Gallus gallus domesticus*‡	Domestic chicken	Namibia	Maritz & Maritz (2020)
Naja annulifera	Snouted cobra	*Gallus gallus domesticus*‡ (6)	Domestic chicken	South Africa; Zimbabwe	Pitman (1958b); Broadley (1959); Newman (1965); Haagner (1993); Shine et al. (2007); Otto (2020)†
		Unidentified	-	South Africa	Hewitt & Power (1913)
Naja haje	Egyptian cobra	*Gallus gallus domesticus*‡ (2)	Domestic chicken	Kenya; Sudan	Corkill (1935); Pitman (1958b)
Naja kaouthia	Monocled cobra	*Anas platyrhynchos*	Mallard	Thailand	Chaitae (2011)
		Dendrocygna javanica	Lesser whistling duck	Thailand	Chaitae (2011)
Naja melanoleuca	Central African forest cobra	*Chroicocephalus cirrocephalus*	Gray-hooded gull	Uganda	Pitman (1958b)
		Gallus gallus domesticus‡	Domestic chicken	Uganda	Pitman (1958b)
		Unknown duck	-	Uganda	Pitman (1962a)
Naja mossambica	Mozambique spitting cobra	*Gallus gallus domesticus*‡	Domestic chicken	South Africa	Maritz & Maritz (2020)
Naja naja	Spectacled cobra	*Gallus gallus domesticus*‡	Domestic chicken	Sri-Lanka	Pitman (1962a)
		Numida meleagris	Helmeted guineafowl	Sri-Lanka	Pitman (1962a)
Naja nigricincta	Western barred spitting cobra	*Nymphicus hollandicus*‡	Cockatiel	Namibia	Theart (2020)†
Naja nigricollis	Black-necked spitting cobra	*Anser domesticus*‡	Domestic goose	Zambia	Maritz & Maritz (2020)
		Columba guinea	Speckled pigeon	Kenya	Pitman (1958b)
		Gallus gallus domesticus‡ (2)	Domestic chicken	Zimbabwe	Pitman (1958b); Pitman (1962a)
Naja nivea	Cape cobra	*Burhinus capensis*	Spotted thick-knee	South Africa	Pitman (1962a)
		Coturnix coturnix	Common quail	South Africa	Stander (2021)†
		Eupodotis caerulescens	Blue korhaan	South Africa	Pitman (1962a)
		Gallus gallus domesticus‡	Domestic chicken	South Africa	Heyns & Smith (2018)†
		Philetairus socius (3)	Sociable weaver	South Africa	Maclean (1973); Covas et al. (2008); Greuel (2020)
		Pterocles namaqua (2)	Namaqua sandgrouse	South Africa	Pitman (1962a); Lloyd et al. (2001)

		Upupa epops	Eurasian hoopoe	South Africa	Layloo et al. (2017)
Notechis scutatus	Tiger snake	Unidentified	-	Australia	Shine (1987a)
Pseudechis australis	Mulga snake	Unidentified	-	South Australia	Shine (1987b)
Walterinnesia aegyptia	Desert cobra	*Dendrocopos syriacus*	Syrian woodpecker	Palestine	Al-Safadi (2004)
Psammophiidae					
Malpolon monspessulanus	Montpellier snake	*Burhinus oedicnemus*	Spotted thick-knee	Spain	Solis & De Lope (1995)
		Carduelis carduelis	European goldfinch	Spain	Monrós (1997)
		Carduelis chloris	European greenfinch	Spain	Monrós (1997)
		Emberiza cirlus	Cirl bunting	Spain	Monrós (1997)
		Turdus merula	Eurasian blackbird	Spain	Monrós (1997)
		Unknown heron	-	Spain	Pitman (1962a)
Psammophis phillipsi	Phillips' whip snake	*Merops breweri*	Black-headed bee-eater	Gabon	Schmidt & Branch (2005)
Psammophis schokari	Schokari Sand Racer	*Pterocles orientalis*	Black-bellied sandgrouse	Morroco	Znari et al. (2008)
Pseudaspididae					
Pseudaspis cana	Mole snake	*Haematopus moquini*	African oystercatcher	South Africa	Calf (2004)
		Larus hartlaubii	Hartlaub's gull	South Africa	Dyer (1996)
		Numida meleagris (2)	Helmeted guineafowl	South Africa	Dyer (1996); Van der Westhuizen (2020)†
		Pavo cristatus	Indian peafowl	South Africa	Maritz & Maritz (2020)
		Prinia maculosa	Karoo prinia	South Africa	Nalwanga et al. (2004)
		Spheniscus demersus	African penguin	South Africa	Dyer (1996)
		Unidentified	-	South Africa	Maritz & Maritz (2020)
Pythonidae					
Liasis fuscus	Water python	Unidentified	-	Australia	Shine & Slip (1990)
Morelia spilota	Carpet python	*Anser anser* (2)	Graylag goose	Australia	Shine & Fitzgerald (1996); Fearn et al. (2001)
		Gallus gallus	Red junglefowl	Australia	Fearn et al. (2001)
Python bivittatus	Burmese python	*Aramus guarauna*	Limpkin	USA	Dove et al. (2012)
		Eudocimus albus	White ibis	USA	Orzechowski et al. (2019)

		Numida meleagris domesticus‡	Domestic guineafowl	USA	Dove et al. (2012)
		Unidentified	-	USA	Dove et al. (2012)
Python natalensis	Southern African python	*Alopochen aegyptiaca*	Egyptian goose	South Africa	Alexander (2012)
		Numida meleagris	Helmeted guineafowl	South Africa	Koen (2021)†
Python sebae	African rock python	Unknown goose	-	-	Spawls et al. 2018
Viperidae					
Bothriechis schlegelii	Eyelash viper	Unidentified (2)	-	Argentina; Trinidad and Tobago	Skutch (1985); Menezes & Marini (2017)
Echis carinatus	Saw-scaled viper	*Argya caudata*	Common babbler	Iran	Moosavi et al. (2011)
Sistrurus catenatus	Massasauga	*Chondestes grammacus*	Lark sparrow	USA	Brush & Ferguson (1986)
		Colinus virginianus	Northern bobwhite	USA	Applegate (1995)
Vipera berus	European adder	*Linaria cannabina*	Common linnet	United Kingdom	Pitman (1962a)

†Unpublished Facebook record

‡Domesticated bird

2.4.3 Body lengths and habitat use of oophagous snakes

Oophagous snakes averaged 2057 mm in maximum length, ranging by an order of magnitude in size from 600 mm (*Denisonia devisi*) to 6000 mm (*Python bivittatus*). However, most of these species ranged between 1500 and 2000 mm in maximum length. The distribution of maximum body lengths of oophagous snakes differed significantly to snakes in general (D = 0.671, $P < 0.001$; Fig. 2.4a). Oophagous snakes were significantly larger in maximum length on average compared to other snakes (Phylogenetic ANOVA: $F_{1,\,3501} = 307.322$, $P < 0.001$). Body size thus appears to be an important component of bird egg consumption by snakes.

Most snake species in my list were terrestrial (60% of all 123 taxa) rather than semi-arboreal (21% of all 123 taxa) or arboreal (17% of all 123 taxa). Only two species (*Laticauda colubrina* and *Thamnophis hammondii*) were aquatic (~2% of all 123 species), and none of the species in my list was fossorial. I found no differences in the body sizes of snakes of differing habitats (Phylogenetic ANOVA: $F_{3,\,105} = 2.117$, $P = 0.339$). Thus, differences in body size of oophagous and non-oophagous snakes are unlikely driven by differences in habitat use. Additionally, I found a low phylogenetic signal for oophagy in snakes (Blomberg's K value of 0.065; $P = 0.504$), indicating that this trait evolves independently of phylogenetic relatedness.

2.4.4 Sizes of consumed bird eggs

Consumed bird eggs ranged between 10 mm (zebra finch, *Taeniopygia guttata*) and 58 mm (domestic goose, *Anser domesticus*) in average diameter. Approximately 64% of the eggs consumed by snakes were on average narrower than the mean of this range (24.38 mm, back-transformed from log widths). Overall, the relative distribution of egg diameters did not differ between consumed eggs and other eggs (D = 0.061, P = 0.602, Fig. 2.4b). The same pattern was found when comparing 100 samples randomly drawn from each distribution (D = 0.091,

$P = 0.813$). Moreover, average egg diameters of both groups were statistically similar in size (Phylogenetic ANOVA: $F_{1,\,2342} = 0.570$, $P < 0.723$; Fig. 2.4b).

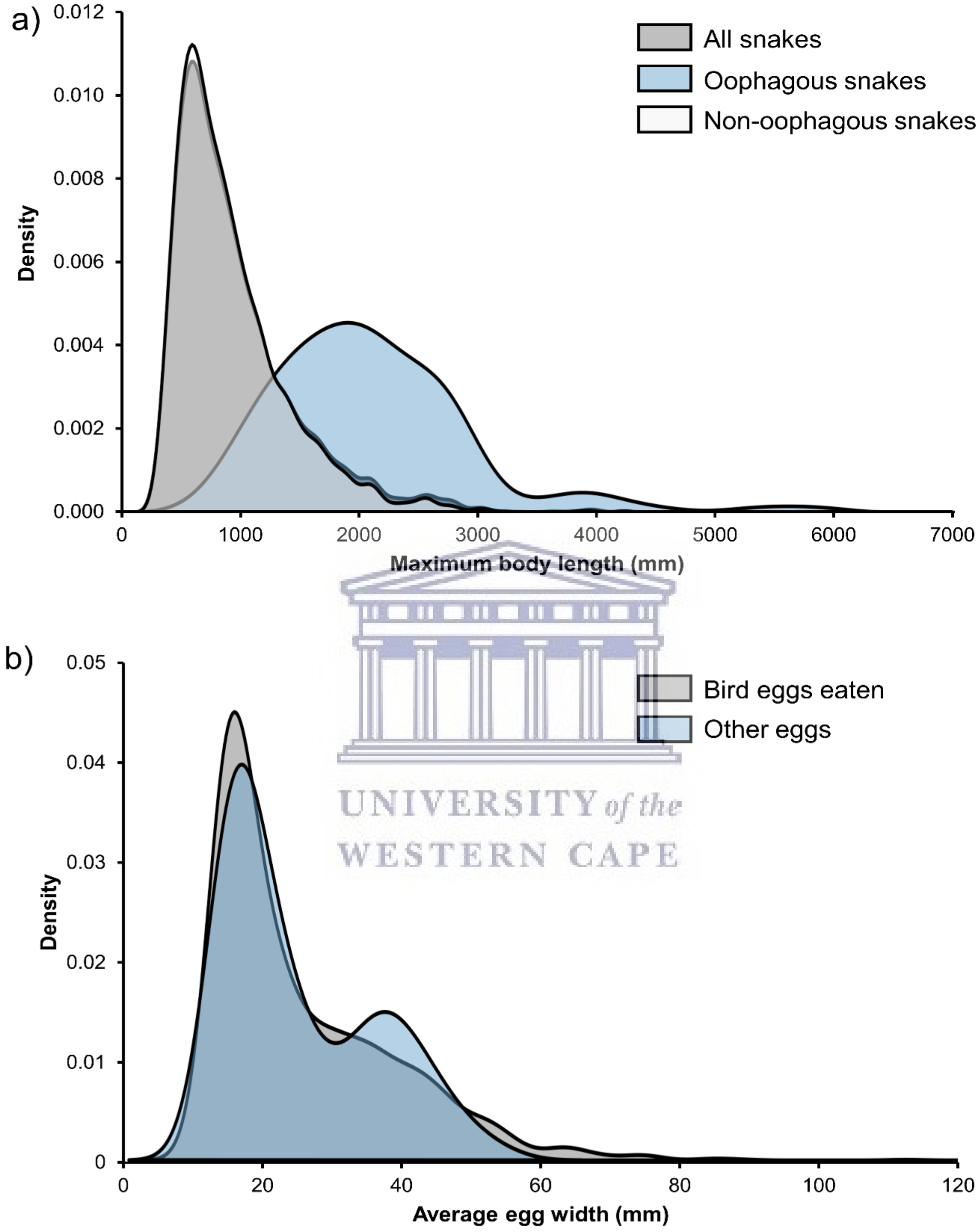

Fig. 2.4: Distributions of a) maximum body lengths (in mm) of all snakes, snakes that consume eggs, and snakes that do not, and b) average diameters of bird eggs (in mm) consumed and not consumed by snakes.

2.4.5 Relationship between snake-size and bird egg-size

Except for *Dasypeltis*, snake species in lower size classes (< 2 m in length) mostly consumed narrow bird eggs (< 20 mm; Fig. 2.5). Larger-bodied species consumed narrow and moderately-sized eggs and some consumed bulkier eggs inaccessible to most other species.

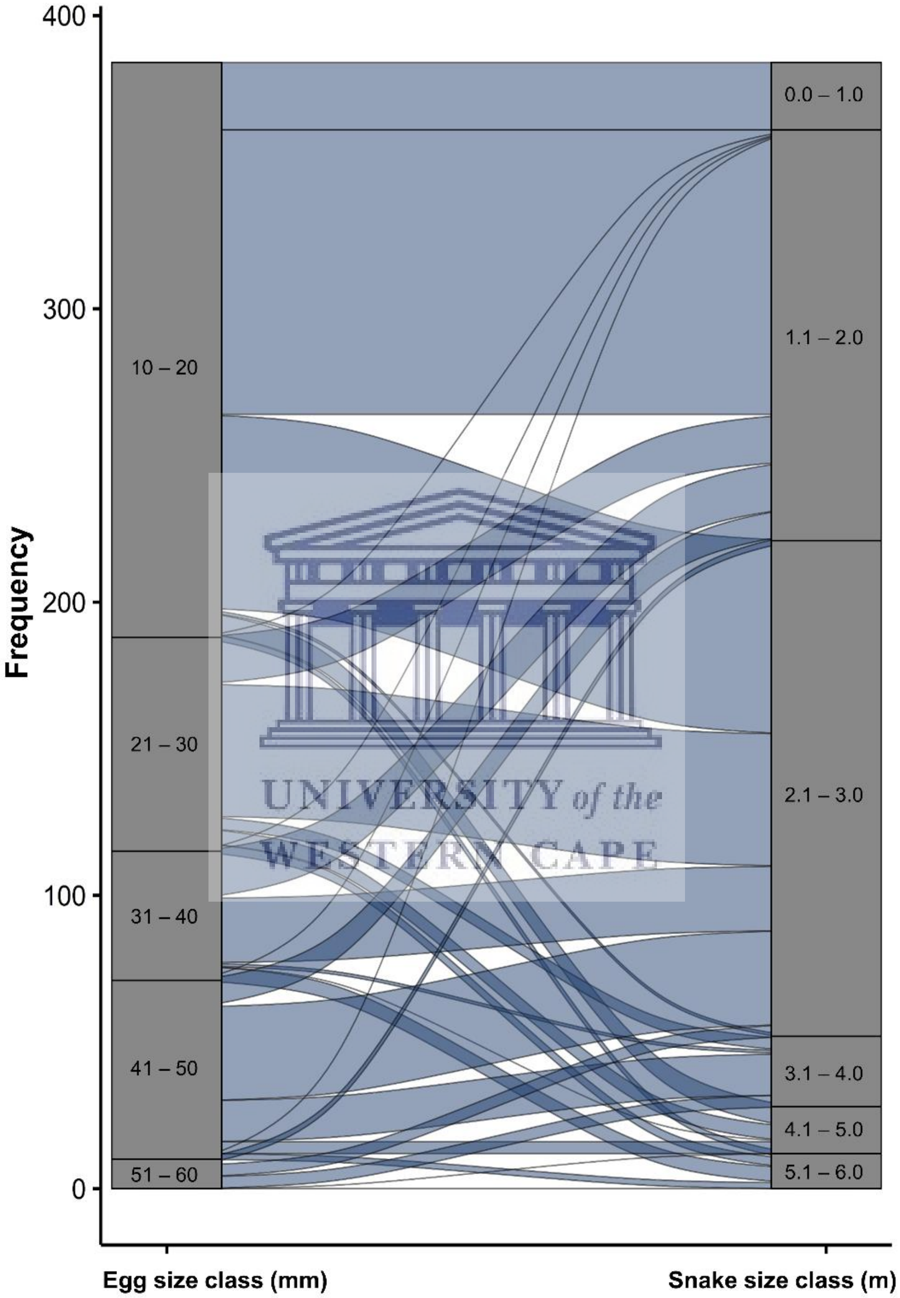

Fig. 2.5: Sankey diagram depicting the association between snake lengths and the widths of consumed bird eggs across 384 reported predation events. All snakes mostly consumed small eggs but only large snakes and *Dasypeltis* consumed bulky eggs.

2.5 Discussion

My search for reports of snakes consuming bird eggs produced 471 feeding records from 238 individual data sources. From those reports, I produced a global list of oophagous snakes spanning 123 species, 58 genera, and seven families. My list greatly exceeds prior attempts at cataloguing predatory interactions between snakes and bird eggs but is similarly geographically biased to a few well-sampled regions. For instance, I compiled nearly five times more records of snakes consuming bird eggs than Grundler (2020), 98 records across 50 snake taxa, but 60% of the records were from North America and southern Africa together. Collectively, the snakes on my list consumed the eggs of at least 210 species of birds across a variety of different families and orders. My examination of traits of identified snake species and bird egg prey revealed that most oophagous snakes are large-bodied terrestrial species and that narrow bird eggs are most frequently, but not disproportionally, consumed. I identified several trends in the data that I hope will form the basis for testable hypotheses and serve as indicators of sampling bias that needs to be addressed.

2.5.1 What we know about bird egg feeding by snakes

There are currently ~4000 recognized species of snakes (Uetz et al. 2021) distributed across the globe, all of which are predators (Greene 1997, Cundall & Greene 2000). Excluding the 471 species of invertebrate specialist Scolecophidian snakes (i.e. the blind snakes and thread snakes), the vast majority of the remaining 3450 species feed on vertebrate prey. My list of 123 snake taxa represents a meagre 4% of those species. Bird eggs thus appear to be an uncommon source of prey for snakes overall. However, my list is undeniably an under-representation of the full range of snakes that consume bird eggs. Many congeners and close relatives of several taxa in my list almost certainly also consume bird eggs but have yet to be directly reported as doing so. For example, despite all 16 members of the genus *Dasypeltis* being known as obligate bird egg specialists (Bates & Little 2013, Bates & Broadley 2018), I only found feeding records for four of these species.

Unsurprisingly, most of the species on my list were represented by only a handful of feeding records. Only ten species had ten or more records, and nearly half of the species were represented by only a single observation. This paucity of feeding records, of which a large proportion represent apparently novel observations, highlights our limited understanding of bird egg predation by snakes. Moreover, additional factors like method-specific biases in feeding data collection also limit the extent of this knowledge. Several studies have highlighted the propensity at which different sampling techniques can affect the quality and quantity of collected dietary information for snakes (Rodrigues-Robles 1998; Glaudas et al. 2017; Maritz & Maritz 2020). As a result, even the diets of species that are relatively well-studied may be incomplete because the methods used to collect feeding data for those taxa may have been unfavourable towards detecting prey like bird eggs. From this perspective, it is clear that continued reporting of novel feeding records, increased publications of descriptive studies of snake diets, and especially investigations of nest predation will lead to additional identifications of species suitable for inclusion in my list.

Most of the observed predations between snakes and bird eggs took place in the USA. However, at similarly high latitudes east of the Atlantic Ocean, exceedingly few records were reported. Moreover, there were no records at latitudes exceeding 60° N. The paucity of records at high latitudes regions can likely be explained by the limited numbers of snake species that occur in those regions. Snake species richness at high latitudes is relatively low compared to regions closer to the equator and in the southern hemisphere. For example, while there are around 200 species of snakes distributed across the USA there are fewer than 30 species in Canada (Ernst & Ernst 2003). Similarly, in most of northern Europe, there are fewer than 10 species of snakes, and in Russia, there are fewer than 45 species (Uetz et al.

2021). The lack of records from these areas is therefore not surprising given that egg consumption is uncommon in snakes and even in areas with high species richness, there are few records.

External factors unrelated to snake occurrences may also have inhibited records from being published. Several regions with high snake species richness are represented by only a few records of egg consumption (for example, West Africa, North Africa, India, and China). In some of those areas, the financial constraints on publishing may make it difficult to report on observations (see Mekonnen et al. 2021) since it may simply be too expensive to publish, especially for standalone observations like dietary feeding records. Additionally, sampling biases caused by a lack of interest in avian or reptile ecology may also have hindered observations of oophagy being reported.

2.5.2 Why don't more snakes eat bird eggs?

While detailed dietary records are not available for many species (Grundler 2020), the feeding habits of most snakes are either at least generally known or can be inferred from species life-history traits and the diets of their close relatives (Greene 1997, Cundall & Greene 2000). While not without exception, such inferred generalized assertions of snake feeding habits are often supported by detailed dietary studies (Bates & Little 2013; Maritz et al. 2019; Maritz et al. 2021c). Many species of snakes can be ruled out as consumers of bird eggs because they occur in areas where other prey types may be more abundant, easier to forage, or less difficult to consume. Alternatively, these snakes may lack the necessary morphology or physiology to consume eggs. Egg-specialist species like *Dasypeltis* possess unique adaptations that facilitate egg swallowing such as reduced teeth and vertebral modifications (Gans 1952) that most other snakes do not have. Factors like limitations in gape size, active selection of different prey, differences in encounter rates, and variable habitat use each contribute to the selectivity of different prey types, including bird eggs (de Queiroz & Rodríguez-Robles 2006).

My results demonstrate that most snakes that consume bird eggs are large-bodied, exceeding 2000 mm in maximum length. Comparatively, the average maximum length of snakes overall is only ~800 mm (Feldman et al. 2016). Snake body size appears to play an important role in the inclusion of bird eggs in snake diets. Larger snakes tend to have larger gapes, and as a result, larger snakes are generally able to consume bulkier and heavier prey than smaller snakes (Arnold 1993; Cundall & Greene 2000). The ovoid shapes and wide cross-sectional diameters of bulky and non-pliable bird eggs relative to snake head dimensions make them difficult for snakes with small gape sizes to handle and ingest (de Queiroz & Rodríguez-Robles 2006). Some small-bodied species like those in the genera *Dasypeltis* and *Boiga* overcome these mechanical constraints using specialized morphological features (Bates & Little 2013, Dandge & Tiple 2016) but most other small-bodied snakes are morphologically ill-equipped to ingest this type of prey (Gartner & Greene 2008).

The relationship between snake body size and bird egg prey sizes further illustrates the importance of relative prey bulk in facilitating these interactions. Most snakes, including several large-bodied boas and pythons, consumed relatively narrow eggs compared to their own lengths. This pattern reflects the findings of Gartner & Greene (2008) who quantified the egg-eating performance of *Lampropeltis getula* and found that adult specimens could only ingest modestly sized eggs relative to the dimensions of their feeding apparatus whereas juveniles could not ingest eggs at all. Those results highlight the body-size mediated mechanical difficulty of bird egg consumption for snakes and support the general predator-size, prey-size pattern found here. However, this pattern is not without exception given that several snakes consume bulky chicken, duck, and goose eggs.

Apart from body size and gape size limitations, specific predispositions towards hunting particular prey also preclude several species of snakes from predating bird eggs. In snakes, the habit of eating the eggs of an animal tends to arise from first eating the corresponding laying animal (de Queiroz & Rodríguez-Robles 2006; Maritz et al. 2021a). This is thought to be because the eggs of an animal share chemical cues with the parent animal, and so 1) this allows snakes to recognize the eggs as suitable food, and 2) leads to greater encounter rates of those organisms (de Queiroz & Rodríguez-Robles 2006). As a result, because relatively few species of snakes consume birds (Greene 1997; Cundall & Greene 2000), few species consume the eggs of birds because they do not associate them as appropriate prey.

Snakes may also actively exclude bird eggs from their diet in favour of other prey. Relative to their size, bird eggs are filled with calories, lipids, proteins, and water (Sotherland & Rahn 1987) but because of their size and associated high handling costs offer lower energetic payoffs to most other vertebrate prey (Greene et al. 2013). Snakes that prey on bird eggs can compensate for this by eating multiple eggs in a single meal, a trend that my data suggests occurs often. However, most species of birds lay small clutches with few eggs (Baicich & Harrison 2005; Tarboton 2011). Moreover, bird eggs are sedentary and nests are often difficult to locate (Nalwanga et al. 2004). For many species of snakes, the energetic costs of searching for nests with eggs likely outweigh the costs of foraging other, more easily detectable and energetically profitable prey. As a result, it is likely beneficial for most snakes to exclude bird eggs in favour of other prey. In particular, large snakes should theoretically prefer singular, heavy prey items that provide a surplus of energy whereas smaller-bodied snakes probably prefer less bulky prey that are easier to consume (Shine 1991a).

Differences in foraging mode (i.e. active foraging versus ambush foraging) and lifestyle habits between snakes also greatly affect the chances of species encountering sedentary prey like bird eggs (Greene 1997; Alencar et al. 2013). Ambush foraging snakes probably only rarely encounter nesting birds and even less so bird eggs. Similarly, aquatic and fossorial species will encounter bird eggs considerably less often than arboreal and terrestrial species. Surprisingly, the majority of the species in my list were terrestrial rather than arboreal or semi-arboreal. However, I suspect that this is likely an artefact of sampling bias rather than a reflection of true biological patterns as terrestrial snakes are easier to detect than arboreal species (Pizzatto et al. 2007). Additionally, most occurrences of egg predation took place in habitats at low elevations (< 500 m above sea level) which could also be indicative of biased sampling efforts since high altitudes are generally difficult to access.

2.5.3 Importance of identifying snake predators of bird eggs

Identifying the snake predators of bird eggs is a key first step toward understanding the extent of their roles in nest predation and the potential implications thereof (Weatherhead & Blouin-Demers 2004, Lahti 2009; Menezes & Marini 2017). By knowing which snakes occur in a given area and which of those species eat bird eggs, researchers can consider species-specific hypotheses informed by existing knowledge of the demographics, ecologies, and natural histories of those particular species (for example Barends & Maritz 2021). Ultimately, this may lead to investigations that further our understanding of the relative importance of different snakes towards avian breeding success and more broadly, their impacts on ecosystem functioning (Reidy & Thompson 2012; DeGregorio et al. 2016a). Importantly, these investigations can also inform conservation strategies that seek to manage or protect endangered or vulnerable species of birds (Carter et al. 2007; Thompson & Ribic 2012).

My primary objective of this review was to compile a comprehensive list of snake species unambiguously categorized as predators of bird eggs. I hope that this list can act as a baseline for further research seeking to understand patterns of nest predation by snakes and their impacts on avian ecology. By searching through the literature, citizen science reports, and social media, I provide a summary of accounts of bird egg predation by snakes that can act as a foundation for a consolidated database for further research.

2.6 Acknowledgements

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Chapter 3: Dietary Specialization and Habitat Shifts in a Clade of Afro-Asian Colubrid Snakes (Colubridae: Colubrinae)

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3.1 Abstract

Speciation through niche divergence often occurs as lineages of organisms colonize and adapt to new environments with novel ecological opportunities that facilitate the evolution of ecologically different phenotypes. In snakes, adaptive diversification may be driven by the evolution of traits relating to changes in their diets. Accordingly, habitat-mediated differences in prey available to ancestral snakes as they colonized and occupied novel dynamic landscapes are likely to have been a strong selective agent behind the divergence and radiation of snakes across the globe. Using an ancestral reconstruction approach that considers the multivariate nature of ecological phenotypes while accounting for sampling variation between taxa, I explored how diet and macro-habitat use coevolved across a phylogeny of 67 species of Afro-Asian colubrine snakes. My results show that the most recent common ancestor of this clade was likely a dietary generalist that occupied tropical forests in Asia. Deviations from this generalist diet to a variety of specialist diets each dominated by the utilization of single prey types repeatedly occurred as ancestral colubrines shifted from tropical forests to savanna and grassland habitats across Africa. I additionally found that dietary specialist species were on average smaller in maximum length than dietary generalists, congruent with established predator-size, prey-diversity dynamics in snakes. I speculate that adaptive divergence in ancestral colubrines arose as a result of a selective regime that favoured diets comprised of terrestrial prey, and that partitioning of different prey types led to the various forms of dietary specialization evident in these lineages today. My findings provide new insights into the ecological correlates associated with the evolution of diet in snakes, thereby furthering our understanding of snake diversification.

3.2 Introduction

Adaptive radiation is driven by phenotypic evolution in response to different ecological opportunities that lead to rapid speciation and the formation of novel lineages as a result of niche divergence (Wellborn & Langerhans 2015; Schluter 2016; Stroud & Losos 2016). The evolution of new and possibly unique phenotypes among different organisms can be facilitated through several means, chief among which is the colonization of new areas or habitats with different resources (Gavrilets & Vose 2005; Yoder et al. 2010; Stroud & Losos 2016). As organisms invade and adapt to new environments with distinct climates, novel competitor assemblages, and changed ecological resource availability, divergent selective pressures can expedite the evolution of distinct phenotypes and ecological traits among different populations, ultimately resulting in the formation of new species (Yeh & Price 2004; Losos & Mahler 2010; Wagner et al. 2012; Alzate et al. 2020). Elucidating the environmental correlates associated with the evolution of phenotypes and ecological traits of extant organisms and their ancestors can therefore provide key insight into patterns of organismal diversification and the processes behind them.

In snakes, diversification has been strongly influenced by evolutionary shifts in diet (Greene 1997; Rodriguez-Robles et al. 1999; Vincent et al. 2006; Alencar et al. 2013; Fabre et al. 2016). Nearly all of the ~4000 species of snakes (Uetz et al. 2021) distributed across the globe are gape-limited predators that ingest prey whole, and together consume a remarkably diverse range of prey from a range of taxonomic groups (Arnold 1993; Greene 1997). The evolution of the various mechanisms employed by different lineages of snakes to search for, capture, and consume different prey are known to have impacted the evolution of their phenotypic characteristics, including the development and fixation of novel adaptations relating to subduing and swallowing different types of prey (Gans 1952; Kardong 1980; Greene 1997; Jayne et al. 2002; Fabre et al. 2016). Thus, changes in the diets of ancestral snakes to include or exclude different types of prey as a result of selection for or against those particular prey have likely contributed to the origins of several groups of species. In some cases, changes in diet may have been facilitated by novel ecological opportunities afforded by transitions in habitat use (Pough & Groves 1983; Shine 1991a; Pyron & Burbrink 2012; Fabre et al. 2016; Maritz et al. 2021a). Accordingly, exploring the evolutionary relationship between diet and habitat use by snakes can provide important insight towards understanding patterns of their current diversity.

Investigations of the evolutionary dynamics of ecological traits like diet and habitat use are typically done by modelling the evolution of those traits across a phylogenetic tree through ancestral state reconstruction. Ancestral state reconstruction has become a powerful tool that offers an effective means in which to statistically infer changes in phenotypes and ecological traits of extant taxa and their ancestors and has been widely used in macroevolutionary studies over the past three decades (Schultz et al. 1996; Pagel 1999a; Pagel et al. 2004; Gamble et al. 2015; Joy et al. 2016). Several statistical models to reconstruct these otherwise unobservable traits among ancestral organisms are available (for example, Pagel 1994; Pagel 1999b; Pagel & Meade 2006) and have been employed in ecological studies of various taxonomic groups (for example, arthropods: Leschen & Buckley 2007, birds: Odom et al. 2014; Wright et al. 2015, lizards: Whiting et al. 2003, and mammals: Van Heteren & Figueirido 2019). In recent years, several studies have used these methods to investigate trait evolution in snakes (Alencar et al. 2013; Harrington et al. 2018; Portillo et al. 2018; Grundler & Rabosky 2020; Maritz et al. 2021a; Naik et al. 2021).

Most methods of ancestral reconstruction used to model resource use across a phylogeny require that variation in patterns of resource use observed among taxa are first classified into a set of univariate character states (Joy et al. 2016). These univariate states are then assigned to extant taxa based on their observed natural histories and are statistically inferred across ancestral nodes. However, complex multivariate traits, such as diet or habitat use, cannot always be adequately summarized as discrete univariate states without losing important subtleties of their complexity (Grundler & Rabosky 2020; Maritz et al. 2021a). As a result, variation in these traits is often oversimplified into broadly defined character states that do not account for their real-world complexities. Consequently, different species may be assigned to a single state but may exhibit important differences in the manners in which they utilize specific resources. These differences will therefore be unaccounted for within the model. This can result in several challenges in interpreting the projected evolutionary transitions of trait use across a phylogeny and limits the inferences that can be made.

Fortunately, recently developed methods of ancestral reconstruction have sought to account for the challenges of reconstructing complex multivariate ecological traits. Grundler & Rabosky (2020) developed a novel approach to reconstructing ecological traits across a phylogeny that takes into account the multidimensional nature of resource use as well as uneven and finite sampling across taxa. Rather than assigning taxa to oversimplified or poorly characterized univariate states, the above model uses empirical counts of observations of species resource use to infer ecological states without distorting or losing information. The model then simultaneously calculates the proportional utilization of resource use for each identified state and distributes those states across taxa and their ancestors over a phylogeny.

In this study, I use the model of ancestral state reconstruction developed by Grundler & Rabosky (2020) to investigate the coevolution and variation in diet and habitat use across a group of Afro-Asian colubrine snakes. The subfamily Colubrinae is a paraphyletic group comprising approximately 744 species (Uetz et al. 2021) distributed across the globe. Here, I chose to investigate a spatially diverse, monophyletic group (Figueroa et al. 2016) of Asian and African genera (~170 species; Uetz et al. 2021): *Boiga*, *Coelognathus*, *Crotaphopeltis*, *Dasypeltis*, *Dipsadoboa*, *Gonyosoma*, *Lycodon*, *Telescopus*, and *Toxicodryas*. This group includes several wide-ranging taxa that occupy multiple habitat types which may have potentially imposed divergent selective pressures that could have affected the feeding habits of various lineages (Engelbrecht et al. 2020). Together, these snakes consume a wide array of different ectothermic and endothermic prey and vary in diet breadth from species that generalise on multiple prey types to dietary specialists that consume only specific prey types. Moreover, at least one invasion of Africa from Asia (Šmíd et al. 2019; Weinell et al. 2021) occurred within the group, offering an ideal opportunity to investigate the correlative effects of colonization of new habitat on dietary adaptation in snakes. I hypothesize that evolutionary shifts in diets of these genera are likely to have correlated with shifts in habitat as the clade diverged and radiated across Asia and Africa.

I reconstructed diet and habitat states across a phylogeny of 67 species of colubrid snakes and their ancestral nodes. I also tested for patterns of correlated evolution between these states using pairwise correlation analyses. I further contextualized these results by testing for the effects of body size, a known constraint of snake feeding (Cundall & Greene 2000; de Queiroz & Rodriguez-Robles 2006; Vincent et al. 2006), on diet breadth across the clade. While taking into account the phylogenetic relatedness of these species, I tested the hypothesis that larger-bodied colubrines have broader diets than smaller-bodied species, a pattern present within other lineages of snakes (Martins et al. 2002; Shine et al. 2014; Maritz et al. 2021a; Naik et al. 2021).

3.3 Methods

3.3.1 Diet data

I gathered diet data for colubrine snakes of the genera *Boiga*, *Coelognathus*, *Crotaphopeltis*, *Dasypeltis*, *Dipsadoboa*, *Gonyosoma*, *Lycodon*, *Telescopus*, and *Toxicodryas* from published literature sources, verified (i.e. research-grade) community science reports published online via iNaturalist (https://www.inaturalist.org) and the social media network Facebook (collated in Maritz & Maritz 2020), and the ‘Squamatabase’ package in R (Grundler 2020). For each taxon, I summed the total counts of observations of consumed prey from each of the following eight prey categories: amphibians, birds, bird eggs, fish, invertebrates, mammals, reptiles, and reptile eggs. Overall, I gathered 1439 observations of prey items for 67 colubrine snake species. These observations ranged from 3–393 observations per species (Table S3.1).

3.3.2 Habitat data

To gather empirical data on habitat use, I mapped GBIF (https://www.gbif.org) occurrence data for each species (Table S3.2) on World Wildlife Fund (WWF) terrestrial ecoregions (Olson et al. 2001) and extracted ecoregion classifications at each point in QGIS version 3.23 (QGIS Development Team 2020). These ecoregions represented 16 discrete major habitat types distributed across the globe (see Olson et al. 2001). I reduced the number of habitat categories by grouping all tropical forest ecoregions into one category, all temperate forest ecoregions into one category, and all grassland and savanna ecoregions (as already grouped by WWF) into one category. This resulted in a total of six remaining discrete habitat categories: 1) tropical forests, 2) temperate forests, 3) savannas and grasslands, 4) mangroves, 5) deserts, and 6) open scrublands. I gathered 13647 occurrence points across the 67 species, with sampling ranging from 2–3883 records per species (Table S3.3).

3.3.3 Body size data

I collected data on the maximum total body lengths (in mm) for each target species from Feldman et al. (2016). These data are presented in Table S3.4.

3.3.4 Phylogeny construction

I constructed a composite phylogeny of the clade using existing published phylogenies which I combined to form a tree comprising 67 species (Supplemental tree S3.1). Because of its extensive coverage and time-calibrated nature, I used the phylogeny of squamate reptiles published by Zheng & Wiens (2016) as a phylogenetic backbone of my tree. I made several edits based on recently published trees for select groups within the clade (Appendix S3.1). These included modifications to the *Boiga* (Weinell et al. 2021), *Crotaphopeltis* (Engelbrecht et al. 2020), *Dipsadoboa* (Branch et al. 2019) and *Telescopus* (Šmíd et al. 2019) clades.

3.3.5 Reconstruction of diet, habitat use, and body size

Because of their multivariate nature, complex ecological traits like diet and habitat use are often challenging to use in ancestral state reconstructions. A single species can utilize several different prey types and occupy multiple habitats across its distribution. Moreover, each of these components (i.e. prey type or habitat type) can vary in frequency of use for each species. This can make it difficult to adequately summarize such traits as discrete or continuous states, as are frequently used in ancestral state reconstructions, without drastically oversimplifying their complexity (Maritz et al. 2021a). To overcome this issue, I used a recently developed model of ancestral reconstruction that accounts for the multivariate natures of ecological traits using empirical counts of trait-use observations and treating these as probability distributions (Grundler & Rabosky 2020).

The model, described in detail in Grundler & Rabosky 2020), follows a continuous-time Markov chain (CTMC) process within a Dirichlet-multinomial framework. Put simply, the model estimates the numbers of identified ecological states and the states themselves from empirical observations of resource use. Those states are therefore not directly observed. The model assumes that each state is a multinomial distribution rather than a categorical variable, and that observed empirical counts of resource use (for example, diet records) are samples drawn from that distribution. This allows the model to account for uneven sampling variation among taxa and uncertainty regarding the assignment of states to each species. Each species is assigned to a particular state, where the state is a vector of resource use probabilities associated with each resource category (i.e. different prey or habitat types). Consequently, while two or more species may be assigned to a single state, observed counts of their real-world resource use will not necessarily be identical. Following Alencar et al. (2013) and Grundler & Rabosky (2020), I considered states with > 70 specificity for a single prey/habitat use as specialist states.

I performed separate diet and habitat reconstructions using the above model within a Bayesian framework through the ‘Macroevolution’ package (Grundler 2019) in R software v4.1 (R Core Team 2021). For both reconstructions, I kept model parameters in concordance with Grundler & Rabosky (2020). This included running each model with a prior assumption of up to 20 resource states for diet and habitat types respectively. I ran each respective model over 164 000 iterations, with sampling at every 128th iteration after a burn-in of the first 5% of samples.

To investigate the effects of body size on snake diet and snake habitat use respectively, I also reconstructed the evolution of maximum snake body length across the phylogeny. For this analysis, I reconstructed the maximum body length of each species as a continuous trait across the phylogeny under a Brownian motion model of evolution using the anc.ML function in the ‘Phytools’ package (Revell 2012). I also tested for the presence of a phylogenetic signal in body size across the phylogeny by calculating Blomberg’s K (Blomberg et al. 2003) and Pagel’s lambda (Pagel 1999a) using the phylosig function of Phytools. Blomberg’s K values greater than 1 indicate the presence of a phylogenetic signal and therefore strong similarity between closely related species, and values lower than 1 indicate no signal. Pagel’s lambda ranges from 0 to 1, with values close to 1 indicating evidence of a phylogenetic signal.

3.3.6 Correlated evolution of body size, diet, and habitat

To examine the pairwise association between diet and habitat evolution across the phylogeny I tested if correlated transitional patterns of evolution were present between diet and habitat use within a phylogenetic context. Specifically, I tested for correlations between shifts in the multivariate diet and habitat states of each taxon derived from my ancestral reconstructions. I used the discrete module of BayesTraits v.3.0.2 (Pagel & Meade 2006) to test for evidence of correlations between each diet state relative to each habitat state across the phylogeny. For these BayesTraits pairwise analyses, I used both a Maximum Likelihood (ML) and Bayesian approach to run models of trait evolution that assumed that 1) diet and habitat traits evolved independently of each other, and 2) diet and habitat traits evolved together. The ML models produced log-likelihood values as well as derived p-values from log-ratio tests between independent evolution and dependent evolution models.

I ran the Bayesian analyses using a reversible-jump MCMC approach over 10^7 iterations with a sampling period of 1000. I also included a reversible jump hyperprior parameter set to an exponential distribution between 0 and 100 to select priors for this analysis. The Bayesian analyses produce marginal likelihood scores for each model which I used to estimate BayesFactor scores using the equation: 2 x [log-marginal likelihood value of the dependent model - the log-marginal likelihood value of the independent model]. BayesFactor scores over two are considered to represent positive support of correlation, scores greater than five represent strong support, and scores over 10 represent extremely strong support (Pagel & Meade 2006).

I examined the pairwise association between body lengths and diet, and between body lengths and habitat use across the phylogeny in BayesTraits using the independent contrasts correlation module. Additionally, I also compared the average log-transformed maximum body lengths of species across dietary states with a phylogenetic ANOVA using Phytools in R. Finally, I investigated the relationship between the average log-transformed maximum body lengths of snakes categorized in each diet state and the breadths of those states' dietary niche using ordinary least squares regression analysis. I calculated diet niche breadths using Levins' standardized measure of niche breadth (*BA*) (Levins 1968).

3.4 Results

3.4.1 Ancestral reconstructions of diet and habitat

Diet reconstruction analyses revealed the presence of seven distinct multivariate dietary states. These included four specialist states (defined as those in which a single prey type accounts for more than 70% of the diet records; Grundler & Rabosky 2020) and three generalist states (Fig. 3.1). The specialist states were diet state 2 (a diet dominated by reptiles but also includes occasional consumption of amphibians, birds, and rarely, mammals), diet state 3 (a diet dominated by amphibians but with some consumption of mammals), diet state 5 (a diet dominated by reptiles but may rarely include mammals and birds), and diet state 7 (obligate bird egg specialist diet). The remaining three states represented generalist diets recognisable by the consumption of multiple prey types at similar frequencies in each state. These include diet state 1 (a diet characterised by frequent consumption of mammals, reptiles, birds, and bird eggs), diet state 4 (a diet characterised by the consumption of mammals and reptiles), and diet state 6 (a diet characterised by the consumption of birds and their eggs, reptiles, and mammals).

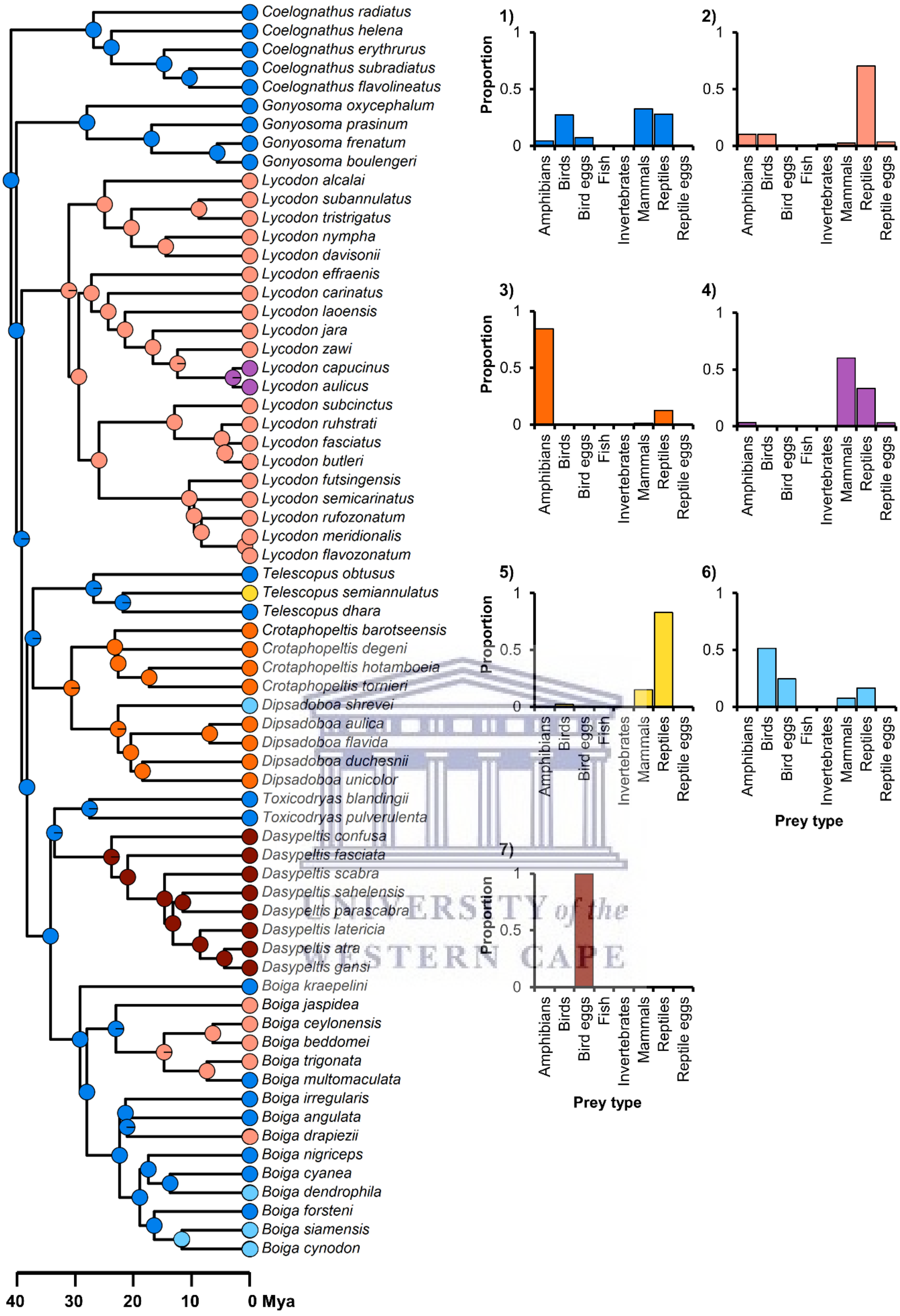

Fig. 3.1: Reconstruction of diet across a subclade of colubrine snakes containing nine genera. Diet states were reconstructed as multivariate probability distributions over eight diet categories. Bar graphs show the proportions of prey for each diet state (1 – 7).

Projections of diet states across the tips of the phylogeny matched the known diets of each taxon as inferred from empirical counts of prey observations (for example, all members of *Crotaphopeltis* were assigned to diet state 3 as amphibian specialists). Reconstructions of diet states across ancestral nodes (Fig. 3.1) suggest that the most recent common ancestor of the snakes in the phylogeny was a dietary generalist that consumed amphibians, birds, bird eggs, mammals, and reptiles (diet state 1). This diet was conserved in all *Coelognathus* and *Gonyosoma*, and the most recent common ancestor of all *Lycodon*, *Boiga*, and the African genera. Across *Lycodon* and *Boiga*, I reconstructed three independent shifts from a generalist diet to a reptile-dominated diet (diet state 2): once by *Lycodon*; once by the *Boiga ceylonensis* group; once by *Boiga drapiezii*. Two species of *Lycodon* (*L. aulicus* and *L. capucinus*) shifted to a diet dominated by mammals and reptiles (diet state 4).

Within the African clades, I reconstructed a single transition from a generalist diet to an amphibian-dominated diet (diet state 3) by the common ancestor of *Crotaphopeltis* and *Dipsadoboa*. All members of these genera retained an amphibian-dominated diet except for *Dipsadoboa shrevei* that reversed to a generalist diet state (diet state 6). Members of the genus *Telescopus* largely retain the ancestral generalist diet, but *Telescopus semiannulatus* shifted towards a reptile-specialist diet supplemented with some consumption of mammals (diet state 5). Similarly, members of the genus *Toxicodryas* retained the ancestral generalist diet, but I note a single transition from the ancestral generalist diet to a specialist diet solely comprised of bird eggs in *Dasypeltis* (diet state 7).

Habitat reconstruction analyses produced 11 distinct multivariate states of habitat use by taxa (Fig. 3.2). Habitat state assignments at tips matched the empirical counts of species occurrence data within the different habitat categories. Habitat states 1 – 4 each represented predominantly closed, tropical forest-dominated states that varied in the proportions with which species utilized other habitat types (habitat state 1: 96% tropical forest use; habitat state 2: 77% tropical forest use; habitat state 3: 82% tropical forest use; habitat state 4: 93% tropical forest use). Similarly, habitat state 5, and habitat states 7 – 10 each represented predominantly open savanna and grassland-dominated states. Habitat state 6 (predominantly deserts and savannas), and habitat state 11 (predominantly tropical forests, temperate forests, and savannas) were generalist in nature.

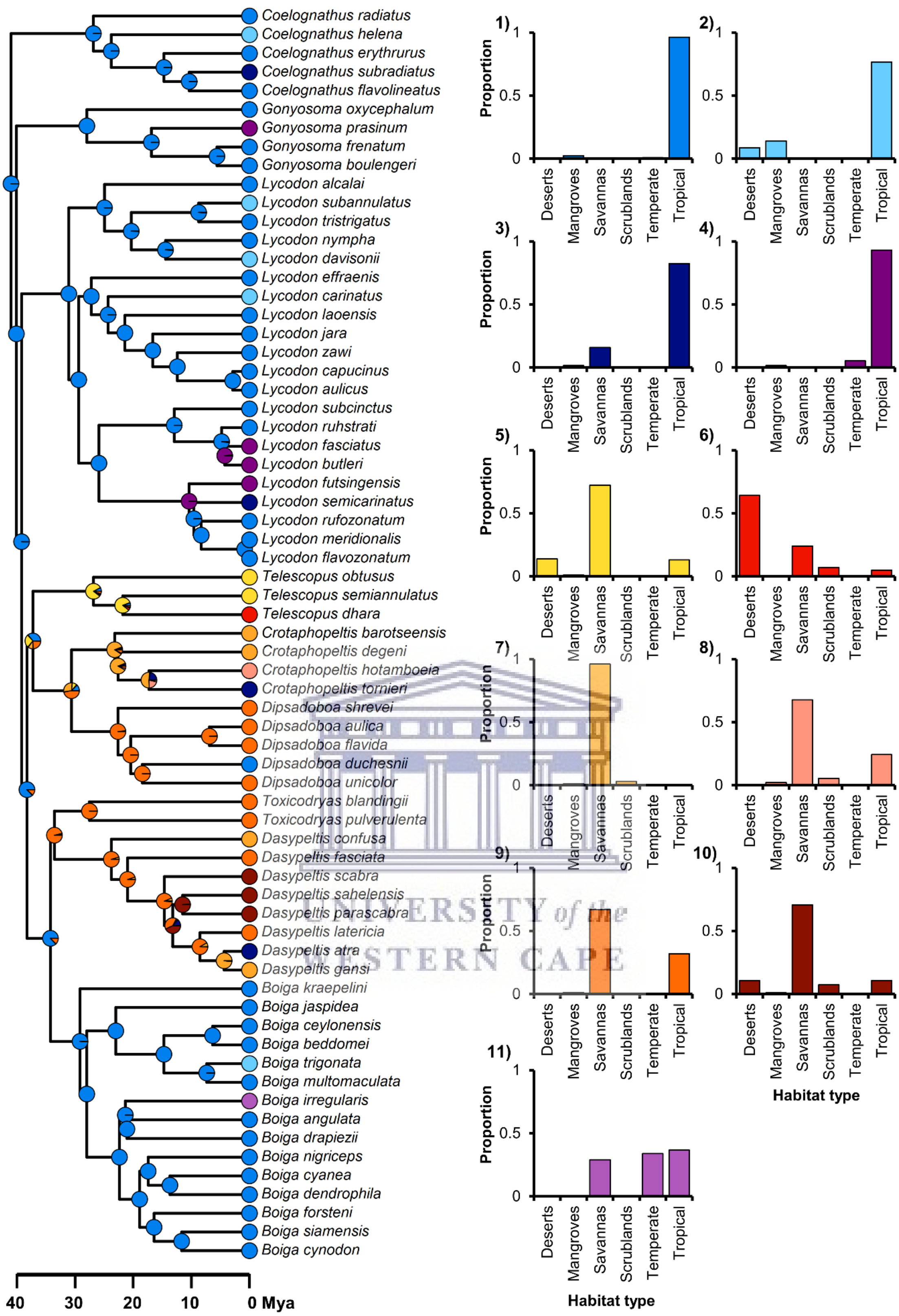

Fig. 3.2: Reconstruction of habitat use across a subclade of colubrine snakes containing nine genera. Habitat states were reconstructed as multivariate probability distributions over six habitat categories. Bar graphs show the proportions of habitat for each habitat state (1 – 11).

Assignments of habitat states across the phylogeny produced similar results to the diet reconstructions. Here, transitions from closed tropical forest-dominated habitat states to those dominated by open savannas and grasslands as the clade diversified repeatedly occurred across the phylogeny. The most recent common ancestor to the clade most likely occupied a tropical forest-dominated habitat with minor use of mangroves. This preference for tropical forests was conserved in all *Coelognathus*, *Gonyosoma*, *Lycodon,* and all *Boiga* except for *Boiga irregularis* which also occupies temperate forests and savannas (in Australia). In the African clades, the majority of species primarily occupy savannas and grasslands, having shifted from tropical forests. The most recent common ancestors of the clade containing *Boiga*, *Dasypeltis, Toxicodryas*, *Crotaphopeltis, Dipsadoboa*, and *Telescopus* predominantly occupied tropical forests but repeatedly transitioned to savannas, grasslands, scrublands, and deserts as the various lineages diversified. Two species, *Dasypeltis atra* and *Crotaphopeltis tornieri* reversed to re-occupy tropical forest habitats. The shift towards a combination of tropical forest and savanna utilization was conserved in both members of *Toxicodryas* and some members of *Dipsadoboa,* with one case of a reversal to full tropical forest occupancy by *Dipsadoboa duchesnii.* One species, *Telescopus dhara,* evolved to primarily occupy deserts.

3.4.2 Correlated evolution of diet, habitat use, and body size

BayesTraits analyses of correlated evolution revealed that shifts in diet across the phylogeny strongly correlated with shifts in habitat use (Table 3.1). Snakes that primarily occupy tropical forest-dominated habitats (habitat states 1 – 4) tend to have generalist diets (diet state 1 and diet state 6) or were reptile specialists (diet state 2). This was prevalent in most of the Asian species (*Boiga*, *Coelognathus*, *Gonyosoma*, and *Lycodon*) but was also retained in *Toxicodryas* and some *Telescopus*. The radiation of species into African savannas and grasslands (habitat types 7 – 10) were significantly correlated with transitions in diet towards amphibian specialization (diet state 3) in *Crotaphopeltis* and *Dipsadoboa*, bird egg specialization (diet state 7) in *Dasypeltis*, and reptile specialization in *Telescopus semiannulatus* (diet state 5).

Table 3.1: Results of BayesTraits analyses of correlated trait evolution of diet and habitat states across the phylogeny. The top rows show Likelihood ratio values with *P* values in brackets and the bottom rows show BayesFactor scores. Significant results are in bold.

Habitat state	**Diet state 1 (generalist)**	**Diet state 2 (reptiles)**	**Diet state 3 (amphibians)**	**Diet state 4 (mammals w/ reptiles)**	**Diet state 5 (reptiles w/ mammals)**	**Diet state 6 (birds w/ bird eggs)**	**Diet state 7 (bird eggs)**
Habitat state 1 (tropical forests)	**10.98 (0.03)**	**22.44 (0.01)**	0.46 (0.98)	**9.86 (0.04)**	0.07 (0.99)	**22.97 (0.01)**	0.62 (0.99)
	11.41	**14.01**	0.40	**8.69**	0.14	**13.87**	1.36
Habitat state 2 (tropical forests w/ mangroves)	0.02 (0.99)	4.77 (0.31)	1.5 (0.83)	0.37 (0.99)	0.04 (0.99)	1.64 (0.8)	2.32 (0.68)
	0.17	0.48	0.38	0.55	1.26	1.30	0.67
Habitat state 3 (tropical forests w/ savannas)	0.02 (0.99)	0 (0.99)	0.82 (0.94)	2.24 (0.69)	0.14 (0.99)	**9.63 (0.04)**	1.17 (0.79)
	0.47	0.20	0.56	1.54	0.34	**6.36**	1.07
Habitat state 4 (tropical and temperate forests)	0.05 (0.99)	2.95 (0.57)	8.13 (0.09)	0.37 (0.99)	0.15 (0.99)	0.63 (0.99)	1.59 (0.81)
	0.23	1.10	2.14	0.94	0.52	2.45	2.02
Habitat state 5 (savannas generalist)	0.37 (0.91)	1.71 (0.99)	0.27 (0.98)	0.07 (0.99)	**8.74 (0.04)**	5.21 (0.27)	0.31 (0.99)
	3.19	0.37	1.26	1.38	**3.84**	1.23	0.08
Habitat state 6 (deserts, savannas, & scrublands)	2.53 (0.64)	0.56 (0.99)	0.29 (0.99)	0.53 (0.99)	0.19 (0.99)	8.14 (0.09)	0.08 (0.99)
	1.17	0.15	0.34	0.61	2.68	3.19	0.73
Habitat state 7 (savannas w/ scrublands)	3.71 (0.45)	5.08 (0.28)	**10.42 (0.03)**	5.09 (0.28)	0.04 (0.99)	0.24 (0.99)	**18.7 (0.01)**
	1.40	1.88	**10.16**	1.96	0.64	1.17	**15.21**
Habitat state 8 (mostly savannas w/ tropical forests)	2.89 (0.99)	0.51 (0.99)	0.18 (0.99)	2.85 (0.58)	0.24 (0.99)	2.23 (0.69)	**23.74 (0.01)**
	0.97	0.10	0.82	1.21	0.40	3.40	**15.82**
Habitat state 9 (savannas & tropical forests only)	2.23 (0.99)	1.63 (0.8)	**14.63 (0.01)**	0.15 (0.99)	0.23 (0.99)	2.41 (0.66)	2.04 (0.73)
	0.17	1.85	**13.14**	1.78	0.38	0.32	0.85
Habitat state 10 (savannas generalist)	2.45 (0.65)	0.84 (0.93)	0.58 (0.96)	0.07 (0.99)	0.06 (0.99)	0.82 (0.99)	0.19 (0.99)
	1.04	0.08	0.52	0.98	0.56	0.97	0.59
Habitat state 11 (savannas, tropical, & temperate forests)	0.82 (0.99)	2.23 (0.69)	0.14 (0.99)	0.31 (0.99)	0.27 (0.99)	0.07 (0.99)	0.04 (0.99)
	1.97	1.85	0.34	1.12	1.04	1.10	0.43

I found strong evidence for phylogenetic signal in body size across the clade (Blomberg's $K = 1.237$, $P < 0.001$; *Pagel's lambda* = 0.961, $P < 0.001$). Evolution of snake body size and diet state strongly correlated with each other (Bayes Factor score = 10.924). Visual inspection of the evolution of body size across the phylogeny (Fig. 3.3) shows that transitions towards smaller maximum body lengths correspond with shifts in diet from generalist states to specialist states, and conversely, shifts towards larger body size were associated with generalist diets.

The results of my phylogenetic ANOVA showed that the average log-maximum lengths of species differed significantly between diet states, particularly between generalist and specialist states ($F_{6, 60} = 9.272$, $P = 0.011$; Fig. 3.4a). Snakes with generalist diets (in particular, diet state 1 and diet state 6) were significantly larger on average than snakes that specialize on a particular type of prey like amphibians (diet state 3) or bird eggs (diet state 7). However, this trend was not present for snakes belonging to the generalist-diet state 4 which were similarly sized to those with specialist diets. Subsequently, I found that the niche breadth of each diet state was positively associated with the average log-maximum body length of species belonging to each respective state ($F_{1, 5} = 12.434$, $P = 0.02$, $R^2 = 0.71$; Fig. 3.4b). Snake body size and habitat use showed only weak evidence for an association between these traits (Bayes Factor score = 0.256).

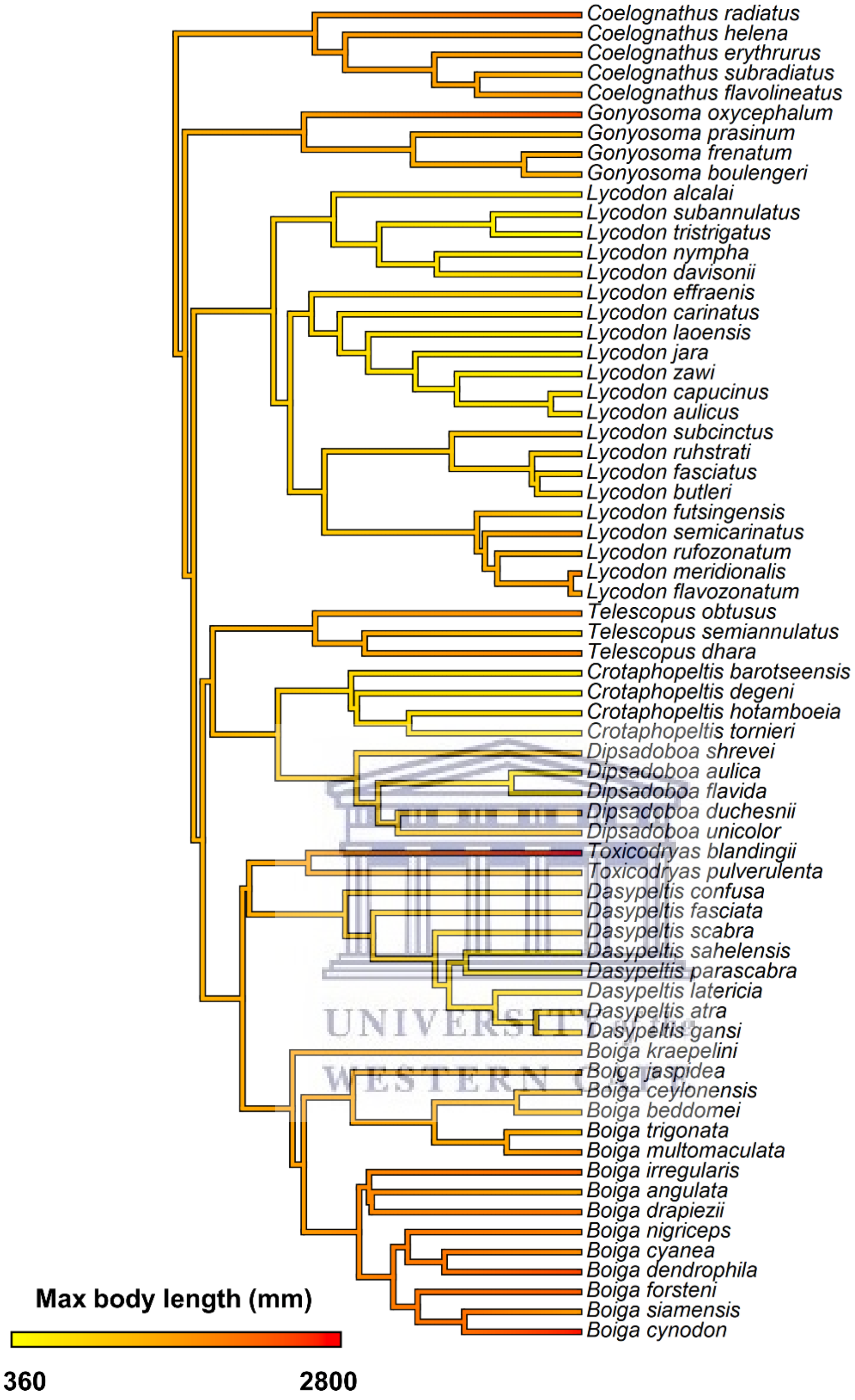

Fig. 3.3: Reconstruction of maximum body lengths (mm) across the subclade of *Boiga*, *Coelognathus*, *Crotaphopeltis*, *Dasypeltis*, *Dipsadoboa*, *Gonyosoma*, *Lycodon*, *Telescopus*, and *Toxicodryas*. Maximum body length was reconstructed as a continuous trait under a homogenous Brownian motion model of evolution.

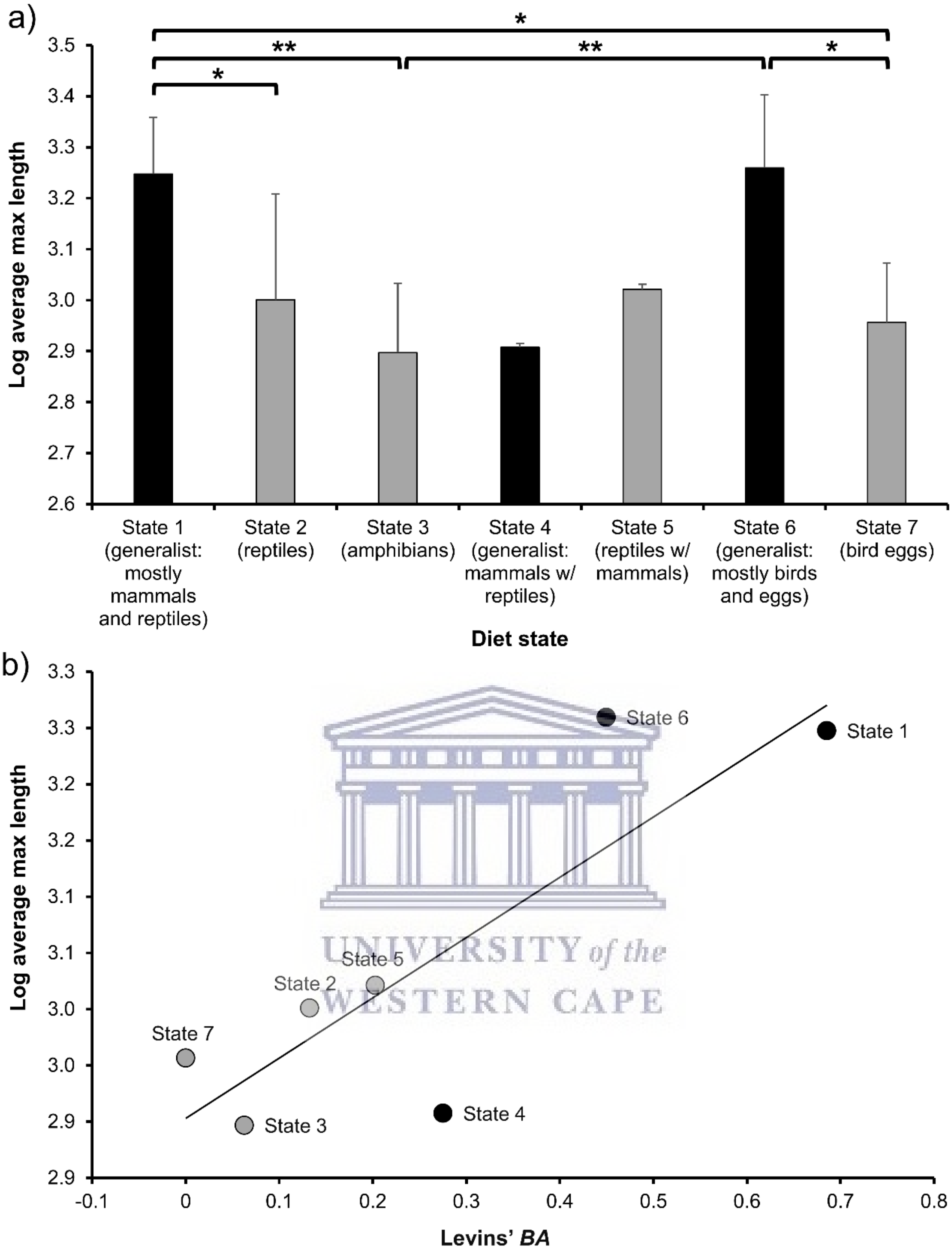

Fig. 3.4: Relationship between log-transformed average maximum body lengths of a group of Afro-Asian colubrine snakes and a) diet state (error bars denote standard deviation) and b) standardized dietary niche breadths. Statistical comparisons are phylogenetic ANOVA results (* $P < 0.05$; ** $P < 0.01$, all other pairwise comparisons are non-significant). Black bars and circles represent dietary generalists; grey bars and circles represent dietary specialists.

3.5 Discussion

My reconstruction of diet evolution across a subclade of the Colubrinae revealed several independent shifts from ancestors with a generalist diet, comprised of mammals, reptiles, birds and their eggs, and amphibians, to an assortment of specialists with diets dominated by single prey types as the clade diversified and expanded. My results suggest that several of these shifts correlated with transitions in habitat use from closed to open environments. This trend was particularly prominent within African lineages where shifts from generalist diets to amphibian-dominated diets (*Crotaphopeltis* and *Dipsadoboa*), bird egg-dominated diets (*Dasypeltis*), and reptiles plus mammal-dominated diets (*Telescopus semiannulatus*) respectively coevolved as these lineages transitioned from inhabiting closed tropical forests to inhabiting open savannas and grasslands. In addition, I also demonstrate that body size has an important association with the evolution of prey utilization by these snakes as I observed a generalized pattern of larger maximum length being correlated with a broader dietary niche. The presence of a phylogenetic signal within the evolution of diet, habitat use, and body size respectively show that the above trends were not present as a result of random distributions of trait evolution across the phylogeny.

3.5.1 Diet and habitat

The relative availability of prey resources within an environment sets the constraints and opportunities for feeding by the snakes occupying that environment. Thus, novel habitats with derived prey resources (both in terms of prey abundances and prey diversity) can provide snakes with divergent ecological opportunities that may ultimately be conducive to the evolution and fixation of unique foraging habits, diets, and adaptive traits associated with specific prey types (Wallace & Diller 1990; Martins et al. 2002; Gartner & Greene 2008; Alencar et al. 2013). My results suggest that the most recent common ancestor of this colubrine subclade was a large-bodied, tropical forest-dwelling species with a generalist diet dominated by birds, mammals, and reptiles, but also including bird eggs and amphibians. This dietary generalist lifestyle remained conserved as the clade diverged and expanded across mainland Asia and nearby off-shore islands, and broad diets were conserved across most members of *Coelognathus*, *Gonyosoma*, and some *Boiga*. However, the ancestor of *Lycodon,* another group of Asian tropical forest dwelling species, shifted to a diet dominated by the consumption of reptile prey. This transition may have been driven by body size constraints, differences in microhabitat use (for example arboreality vs terrestriality; Martins et al. 2002; Harrington et al. 2018), or a combination of both, and reptiles remain the predominant component in the current-day diets of most extant species of *Lycodon*.

The invasion and occupancy of Africa by the clades containing (1) *Boiga*, *Dasypeltis* and *Toxicodryas*, and (2) *Crotaphopeltis*, *Dipsadoboa*, and *Telescopus* ultimately provided the ecological opportunity that led to the evolution of the dietary specialist lifestyles of some of those snakes. Recent evidence suggests that the diversification of these lineages coincided with large-scale transitions in habitat and climate across continental Africa throughout the Oligocene and Miocene epochs (~35 to ~15 million years ago; Šmíd et al. 2019; Engelbrecht et al. 2020). During the Oligocene, most of Africa was dominated by closed forests and woodlands that gradually receded as the continent shifted northwards and the Tethys sea closed (Matthee et al. 2004; Šmíd et al. 2019). Throughout the Oligocene and Miocene, these forests contracted in northern and southern Africa, leaving only fragmented remnants in tropical Africa (Jacobs 2004; Couvreur et al. 2020), resulting in an overall increase in arid conditions throughout most of the continent that facilitated major expansions of open, C_4-dominated plant systems (i.e. grasslands, savannas, scrublands etc., Barlow et al. 2019). Accordingly, the transition from closed to open habitats and assumed habitat-mediated shifts in prey, including reduced abundances of arboreal taxa and an explosion of terrestrial taxa across numerous faunal groups (Couvreur et al. 2020), likely drove major shifts in the diets of the above taxa.

My results point to the ancestor of *Dasypeltis* and *Toxicodryas* as a dietary generalist that preyed upon several taxonomic groups, including a large proportion of birds and their eggs. This diet is conserved in *Toxicodryas* but not in *Dasypeltis*, whose most recent common ancestor unidirectionally transitioned towards an obligate bird egg diet. This result supports the findings of de Queiroz & Rodriguez-Robles (2006) who show that the inclusion of the eggs of an animal within the diet of a snake tends to derive from a diet that includes the parent animal that produces the eggs. Differences in lifestyle habits between *Dasypeltis* and *Toxicodryas* could explain why the latter retained a generalist diet but the former did not. All members of *Toxicodryas* are fully arboreal and occupy a combination of closed and open habitat types (Spawls et al. 2018). Contrastingly, most *Dasypeltis* are terrestrial or semi-arboreal and primarily occupy open habitats (Branch 1998; Bates et al. 2014; Spawls et al. 2018). Open habitats lack the exceptionally large trees associated with tropical forests, and in rare cases may also be devoid of sheltered areas. Birds occupying these habitats are thus forced to build nests close to the ground in low-lying vegetation in many cases (Tarboton 2011; Bates & Little 2013). The combination of an abundance of bird eggs available at ground level, coupled with concomitant decreases in arboreal prey options, is strongly speculated to have produced the ecological circumstances and selective regime that facilitated bird egg specialization in *Dasypeltis* (Gartner & Greene 2008).

The shift from generalist to amphibian-dominated diets in ancestral *Crotaphopeltis* and *Dipsadoboa* (~28 mya) coincided with transitions from forests to open environments. A reptile-dominated diets evolved later in *Telescopus* (~20 mya) within open environments. Dietary transitions in these lineages were likely driven by habitat-mediated shifts in prey availability. In the case of *Crotaphopeltis* and *Dipsadoboa*, a close association with open, mesic environments likely facilitated greater encounter rates of anuran prey (Keogh et al. 2000). Over time, continued consumption of bulky anurans may have contributed to the fixation of proximate factors that determine prey utilization like feeding morphology and foraging kinematics in these snakes (Rasmussen 1997; Keogh et al. 2000; Eniang et al. 2013). Similarly, an association between arid and desert areas in most *Telescopus* (Šmíd et al. 2019) likely facilitated the evolution of their predominantly reptile-orientated diets. Other ecological factors concerning community dynamics involving competition and resource partitioning likely also played a role in the development of these diets (Luiselli et al. 1998; Luiselli 2006a).

3.5.2 Diet and body size

Differences in prey utilization among the colubrines within each of the different dietary groups were strongly associated with differences in their respective maximum body lengths. Species that deviated from the ancestral generalist diet were on average smaller than those for which the generalist diet was conserved. Moreover, mechanically difficult to ingest prey like birds and mammals with wide cross-sectional diameters (de Queiroz & Rodriguez-Robles 2006; Close & Cundall 2012; Wiseman et al. 2019) were absent or limited in the diets of smaller-bodied species. Thus, my results suggest that in addition to habitat-linked prey availability, body size also plays an important role in determining the diets of colubrines. This pattern is also evident in other groups of snakes. In an analysis of the evolution of diet in lamprophiid snakes, Naik et al. (2021) found a similar relationship between body size and diet breadth whereby most large-bodied species of lamprophiids consume a broad array of different prey but smaller-bodied species only consumed arthropods and invertebrates.

3.5.3 Further hypotheses and outlook for macroevolutionary studies of snakes

Several testable hypotheses can be derived from my findings and the interpretations of my results. Importantly, my results show that transitions in diet from generalist to specialist states occurred repeatedly across the phylogeny. Overall, diet is largely conserved across the colubrines within this subclade but repeatedly shifted as ancestral species adapted both ecologically and morphologically to occupy open habitats with presumed variation in prey resources. Because this transition from closed habitat, dietary generalist to open habitat, dietary specialist occurred several times across the phylogeny rather than just once, it suggests that shifts in habitat, and likely changes to prey resources, was a strong selective agent behind the evolution of diet and diversification of several lineages of colubrine snakes. Identification and quantification of ancestral prey availability across African and Asian habitats through time and space could provide valuable context for understanding the evolution and adaptive diversification of these colubrines and other snakes (Gartner & Greene 2008; Barlow et al. 2019).

Although we are unlikely to ever know much about ancestral communities in terms of population densities, determining the numbers of species of different ancestral prey groups concurrent with colubrine radiation could offer some form of approximation for prey availability that could help explain the evolution of dietary specialization. Gartner & Greene (2008) speculate that radiations of small-bodied birds across Africa, including the Fringillidae and Estrildidae families (Barker et al. 2004) resulted in small-sized bird eggs being amply available for ancestral *Dasypeltis*, leading to the eventual adaptation of their bird egg-specialist lifestyle. I postulate that similar radiations of amphibians or lizards, and resultant increases in abundances of those prey, could have facilitated adaptive dietary specialization in *Crotaphopeltis*, *Dipsadoboa*, and some *Telescopus* respectively. However, it is possible that these snake genera evolved independently of the diversification of their preferred prey types and originated long before or after explosive radiations of those groups across Africa.

Moreover, these shifts in diet may have been derived as a result of other factors like competition and resource partitioning. Investigations of these snakes' feeding performance and kinematics towards different prey could substantiate my claims of adaptive radiation.

My finding that diet breadth correlates with body size in colubrines is congruent with existing trends in diet breadth associated with predator-size, prey-diversity relationships in snakes (Shine 1991b; Arnold 1993; Vincent et al. 2006). However, this pattern was not without exception, as my results showed that two small-bodied (~ 800 mm) species of *Lycodon*, *L. aulicus* and *L. capucinus*, are both dietary generalists. These two species diverged from the reptile-dominated diet observed in most other *Lycodon* and are the only species assigned to diet state 4 (predominantly mammals and reptiles). It is thus unclear if the correlation between diet breadth and body size is present as a result of some lineages evolving towards an optimal size suited for consuming particular prey types, or if ancestral species were morphologically size-constrained and obligately excluded bulky prey types. Interspecific comparisons of adaptive performance, morphology, and fitness of snakes could provide further details on these dynamics.

As with all ancestral reconstruction analyses, the accuracy of my results hinged on the strength of the taxonomic coverage of the phylogeny, the topology of the tree, and the quality of input trait information (Joy et al. 2016; Grundler & Rabosky. 2020). The 67 taxa included in the phylogeny represent a reasonably meaningful sample size (Li et al. 2008) with adequate representation of species across each genus given the poorly catalogued ecologies of several members of this group of snakes (Li et al. 2010). Moreover, the taxonomic relationships among taxa in my composite phylogeny are well-supported across recent taxonomic studies and revisions of colubrines (Bates & Broadley 2018; Šmíd et al. 2019; Engelbrecht et al. 2020; Weinell et al. 2021). While proportions of habitat use are simple to obtain from species occurrence data, dietary information is often scarcer. However, the diets of the species in the phylogeny are, in most instances, relatively well-catalogued compared to similar studies (Alencar et al. 2013; Grundler & Rabosky 2020; Maritz et al. 2021a; Naik et al. 2021). Overall, my results should therefore represent a reasonably accurate reflection of the evolution of diet and habitat dynamics across this group, and I do not expect that the broad trends of my findings would change with increased coverage.

Broadly, my approach towards elucidating the coevolution of ecological traits in colubrines through the use of ancestral state reconstructions was successful and promotes the use of such methodologies for macro-evolutionary studies of snakes in general. However, the issue of data availability and data quality remains a challenge for many lineages of snakes that remain poorly studied. Fortunately, these challenges may be resolved as new information becomes accessible. The continued, rapid publication of studies of snake systematics (for example Broadley et al. 2018; Portillo et al. 2018; Hallerman et al. 2020) has and continues to resolve problematic taxonomies of several lineages of snakes. Moreover, many avenues for the continued publication of snake ecological data remain available, and increased popularity in the use of novel outlets such as online databases and community science projects provide a positive outlook towards increased access and availability of species natural history information. Ancestral reconstructions remain a powerful tool with which to study shifts in resource use changes in ecological traits, and advances in these methods are a boon for the field of macro-evolution.

3.6 Acknowledgements

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Chapter 4: Spatio-Temporal Variation in Prey Availability Does Not Preclude Dietary Specialization By African Egg-Eating Snakes (*Dasypeltis scabra*) in Southern Africa

4.1 Abstract

The evolution of ecological specialization on a restricted set of resources requires that those resources are available when needed by an organism. Moreover, when morphological traits make resource access body size-dependent, changes in resource availability might disproportionately alter access to those resources for different cohorts within a population. I investigated patterns of variation in prey resources available for consumption by southern African *Dasypeltis scabra*, an obligate bird-egg specialist snake. In a laboratory study, I tested the limits of the ingestion ability of fourteen *D. scabra* of varying sizes. Using these data, I identify the bulkiest eggs that snakes of different sizes can ingest and compare these to monthly size distributions of available bird eggs in the region. I estimate that adult *D. scabra* can consume the eggs of 708 of 728 bird species (98%) in southern Africa whereas neonates can consume the eggs of 363 species (50%). Additionally, I demonstrate that bird breeding seasonality causes heterogeneity in the availability of eggs throughout the year. Eggs are less frequently available during winter months, but widely available during warmer months. This seasonal difference in availability is far greater for smaller-bodied snakes. These temporal constraints on prey availability that sometimes make prey ephemerally available are probably the source of the selective pressures that contributed to increased ingestion ability (so that smaller snakes could potentially access larger eggs that are more readily available through cooler months) and reduced metabolic rates in *D. scabra* (which allow snakes to fast during periods of limited availability of food). Lastly, I speculate that in environments where bird breeding is rainfall dependent, but rainfall is unpredictable, the unpredictable nature of the availability of eggs may exclude *Dasypeltis*.

4.2 Introduction

All species utilize a subset of abiotic and biotic resources to fulfil their ecological needs (Futuyma & Moreno 1988; Devictor et al. 2010; Forister et al. 2012). Moreover, the extent to which species are specialist or generalist in their use of available resources has important consequences for their ecology and community interactions. In extreme cases, species may obligately specialize on a single set of resources to the exclusion of others (Forister et al. 2012). However, specialization on a specific set of resources requires that those resources are available when needed by the organism. Consequently, obligate specialists are often at greater risk of extinction compared to other species (Vázquez & Simberloff 2002; Devictor et al. 2010). As a result, the evolution of ecological specialists tends to occur more often in stable environments with reliable resource availability (Colles et al. 2009; Clavel et al. 2011).

The rhombic egg-eater, *Dasypeltis scabra*, is a widespread species of medium-sized (snout-vent length (SVL) range: 160 – 1000 mm; Bates & Broadley 2018) colubrid snake that occurs throughout most of southern and east Africa (Bates et al. 2014, Bates & Broadley 2018; Spawls et al. 2018). These snakes are specialist, obligate consumers of bird eggs (Bates & Little 2013) —a type of prey that is functionally difficult for most, but especially small-bodied, snakes to consume (de Queiroz & Rodriguez-Robles 2006; Gartner & Greene 2008; Barends & Maritz 2022a) mostly because of their bulky sizes. Prey bulk (i.e. the cross-sectional diameter of the prey) represents a major constraint of ingestion that can limit the breadth of snake diets (Close & Cundall 2012). Large egg-eaters are known for their extraordinary feats of ingestion of bulky bird eggs (Bates & Little 2013). However, neonate *Dasypeltis* are small (SVL = 160 – 200 mm, mass = ~3 – 4 g, head width = ~5 mm) and young snakes are likely to face significant morphological constraints in which eggs they can consume. Thus, finding appropriately-sized eggs to consume may prove difficult for small snakes. The purported scarcity or even absence of suitably-sized eggs in some areas has led to speculation that newly hatched *Dasypeltis* individuals potentially eat other eggs such as those of invertebrates, geckos, or other snakes (Bates 1990).

Given the potential constraints to obligate bird egg consumption, *Dasypeltis scabra* offers an ideal opportunity to investigate the link between ecological specialization and resource availability. This is because bird eggs are a taxonomically diverse but functionally identical prey resource. All bird eggs are calcareous, smoothly textured, and roundly/oval-shaped (Tarboton 2011), and therefore offer similar constraints of ingestion when accounting for variation in size. Moreover, many species of birds breed only seasonally (Hockey et al. 2005; Tarboton 2011) and so eggs of differing sizes are likely to show seasonal fluctuations in abundance. Specifically, we can ask whether bird breeding seasonality and therefore resource availability, has the potential to preclude obligate specialization by reducing resource availability for snakes of smaller body sizes.

I thus investigated variation in the patterns of bird egg availability and accessibility for consumption by *Dasypeltis scabra* across southern Africa. In the laboratory, I quantified the ingestion ability of *D. scabra* to identify the bulkiest eggs that individuals of different sizes can ingest. I also tested the hypothesis that egg-eaters exhibit ontogenetic shifts in their feeding preferences by offering adults and juveniles eggs of varying sizes. I then used that information to infer which bird species are producing accessible prey for differently sized egg-eaters based on published bird egg sizes. Lastly, I assess patterns of spatio-temporal variation in the availability of differently sized bird eggs deposited monthly across the region.

4.3 Methods

4.3.1 Ingestion ability of Dasypeltis scabra

I housed 14 wild-caught individual *Dasypeltis scabra* from Cape Town, South Africa. These individuals ranged in age from neonates to fully matured adults. Snakes were kept under a natural light regime within a laboratory at the University of the Western Cape. Temperature was not kept constant and ranged from 15.2 – 25.6°C throughout the study. Each neonate or juvenile snake was housed individually within an enclosure measuring 260 x 350 x 120 mm and each adult was housed in a cage measuring 420 x 600 x 200 mm. I placed paper towels in each enclosure to act as substrate and I included folded newspaper and cardboard to provide snakes with refugia. I provided snakes with water *ad libitum* in ceramic water bowls.

Between April 2019 and April 2021, I offered snakes a range of bird eggs acquired from local breeders. They included the eggs of Cape sparrows (*Passer melanurus*), Chinese painted quails (*Excialfactoria chinensis*), common quails (*Coturnix coturnix*), diamond doves (*Geopelia cuneate*), domestic chickens (*Gallus domesticus*), domestic ducks (*Anas platyrhynchos domesticus*), domestic geese (*Anser anser*), German roller canaries (*Serinus canaria domesticus*), king pigeons (*Columba livia domestica*), Muscovy ducks (*Cairina moschata*), rock doves (*Columba livia*), speckled pigeons (*Columba guinea*), West Peruvian doves (*Zenaida meloda)*, and zebra finches (*Taeniopygia guttata*). These eggs ranged in size from 10.90 mm diameter (mass = 0.68 g) to 56.27 mm diameter (mass = 159.12 g). Snakes were offered eggs at least once per month and I typically offered multiple eggs per meal depending on egg availability.

Before each meal was offered, I measured the diameter of each egg (in mm) using digital callipers and the snout-vent length of each snake (in mm) using a standard measuring tape. To calculate the ingestion ability of egg-eaters, I offered eggs of varying sizes including eggs that were perceived to be too bulky or too small and recorded whether or not the snakes consumed those eggs. I then regressed egg-eater SVL against the diameters of all consumed eggs using quantile regression to identify the upper (99% quantile) and lower (1% quantile) limits of snake ingestion ability. Quantile regressions were performed using the ‘Quantreg’ package (Koenker et al. 2018) in R software v 4.1 (R Core Team 2021).

4.3.2 Spatial variation of bird egg availability

I used checklists from the second Southern African Bird Atlas Project (SABAP2; Underhill et al. 2017) to create bird species lists for southern Africa. I refer to southern Africa to include Botswana, Malawi, Mozambique, Namibia, South Africa, Zambia, and Zimbabwe. The SABAP2 database contains thousands of checklists of detections of bird species derived from multiple standardized surveys within fixed pentad grid cells (approximately 61 km^2) spatially distributed across southern Africa (Hugo & Altwegg 2017; Underhill et al. 2017). I collected data on the egg diameters (in mm) and laying months from Tarboton (2011) for each bird species detected in SABAP2 checklists. I opted to exclude data for ostriches (*Struthio camelus*) as ostrich eggs are overtly too bulky (average diameter = 121 mm) for consumption by *Dasypeltis scabra*. I compared the sizes of eggs deposited by southern African birds using kernel density estimates of egg diameters and performed several, separate Kolmogorov-Smirnov tests to compare the size distributions of eggs across countries. I also compared log-transformed mean egg diameters across countries via One-way ANOVA tests.

Using the results of the feeding trials in conjunction with size data of bird eggs deposited across southern Africa, I calculated the percentage of eggs accessible to egg-eaters in the region. For these calculations, I compared the number of bird species whose eggs are within the maximum threshold of ingestible size as per the regression line equation derived from the results of my quantile regression analyses.

4.3.3 Temporal variation of bird egg availability

Given the similarities in the suites of bird eggs between the various countries of southern Africa (see Results), I opted to evaluate temporal variation in bird egg availability across the region as a whole rather than for each country individually. For this analysis, I first compared monthly frequencies of breeding bird species using a One-factor Chi-square test. I then compared average egg sizes (log-transformed egg diameters) per month using a One-way ANOVA test to test for monthly differences in egg size. All statistical analyses were performed using R software v 4.1 (R Core Team 2021) and IBM SPSS v 23.0 (IBM 2021).

4.4 Results

4.4.1 Ingestion performance

The snakes in the colony collectively consumed 98 of 234 eggs (~ 42%) offered as meals during feeding trials. No individual consumed every egg offered. Consumed eggs ranged in diameter from 11.12 to 49.61 mm (Fig. 4.1). Snake SVL was strongly correlated with maximum ingested egg size as larger individuals consumed considerably bulkier eggs than smaller individuals (Linear regression: $F_{1,96} = 155.413$, $P < 0.001$, $R^2 = 0.62$). Moreover, the consumption of eggs within the 99th quantile of egg diameters was significantly related to snake SVL (Quantile regression: $F_{1,96} = 13.134$, $P < 0.001$). Based on the regression equation of the above analysis, my data suggests that the largest egg-eaters could feasibly consume eggs as wide as 58.35 mm. Conversely, eggs consumed within the 1st quantile showed no significant relationship to snake SVL (Quantile regression: $F_{1,96} = 0.182$, $P = 0.856$). These results indicate the presence of an ontogenetic telescope in egg size within *Dasypeltis scabra*.

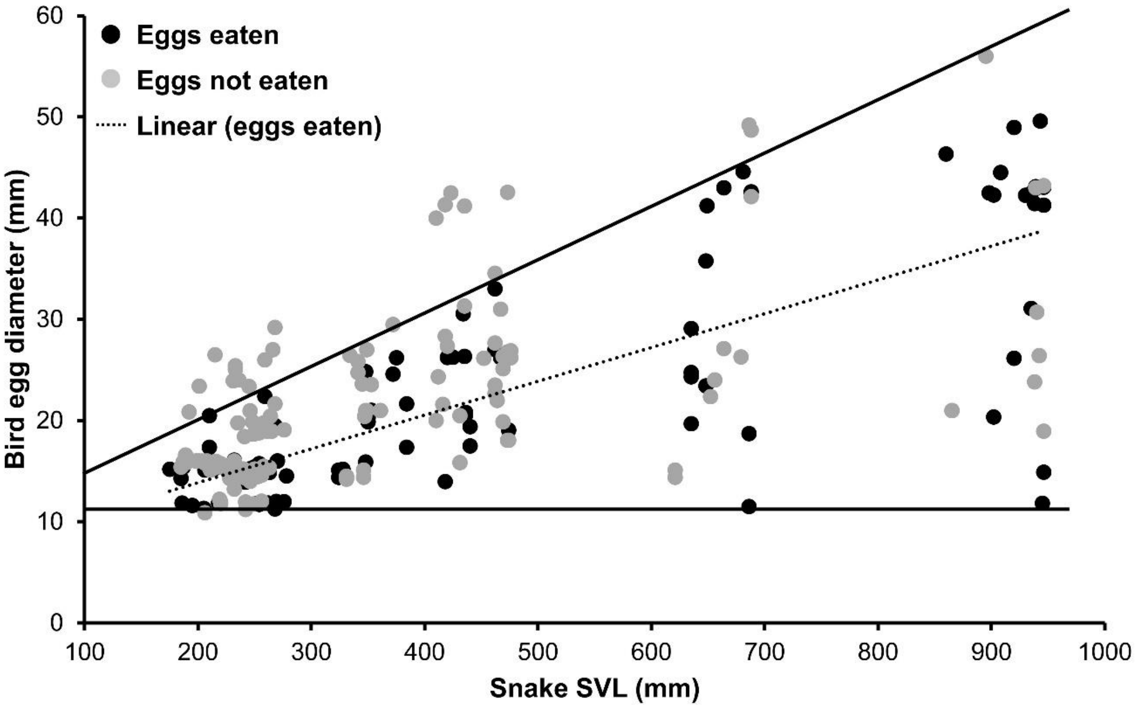

Fig. 4.1: Relationship between eaten (black) and uneaten (grey) egg diameter (mm) and snake SVL (mm) for all offered meals. Solid black lines represent the 1st (bottom) and 99th (top) quantile regression of eaten eggs. The dashed line represents the linear relationship between the sizes of snakes and the sizes of eaten eggs.

4.4.2 Spatial variation in bird egg availability

Country-specific bird species richness significantly differed between countries (Chi-square test: $\chi^2_{df = 6} = 51.305$, $P < 0.001$) but was high throughout the region, ranging from 435 species in Malawi to 640 species in South Africa (Table S4.1). However, despite differences in species richness, the size distributions of the suites of bird eggs were similar across all countries (Kolmogorov-Smirnov tests: $d = 0.010 – 0.054$; $P = 0.429 – 0.999$; Fig. S4.1), ranging from 9.5 mm – 70.6 mm in each case. Additionally, mean egg diameters across countries were also not significantly different (mean egg diameters = 23.78 – 25.12 mm; One-way ANOVA test of Log-egg diameter: $F_{6, 3577} = 0.919$, $P = 0.481$; Post-hoc tests: $P >$ 0.05 in all cases).

Examination of the relationship between snake ingestion ability and the proportion of bird eggs community accessible for consumption revealed a positive relationship between snake body length and food accessibility. As snakes grow in length, the percentage of ingestible eggs of southern African birds increases until a plateau is reached as snakes approach their maximum lengths (Fig. 4.2). The feeding performance of the egg-eaters suggests that hatchling snakes (160 mm SVL) are capable of consuming the eggs of 50% of southern African breeding birds (363 species collectively). Comparatively, this percentage increased to 98% (708 species collectively) for large adults (950 mm SVL).

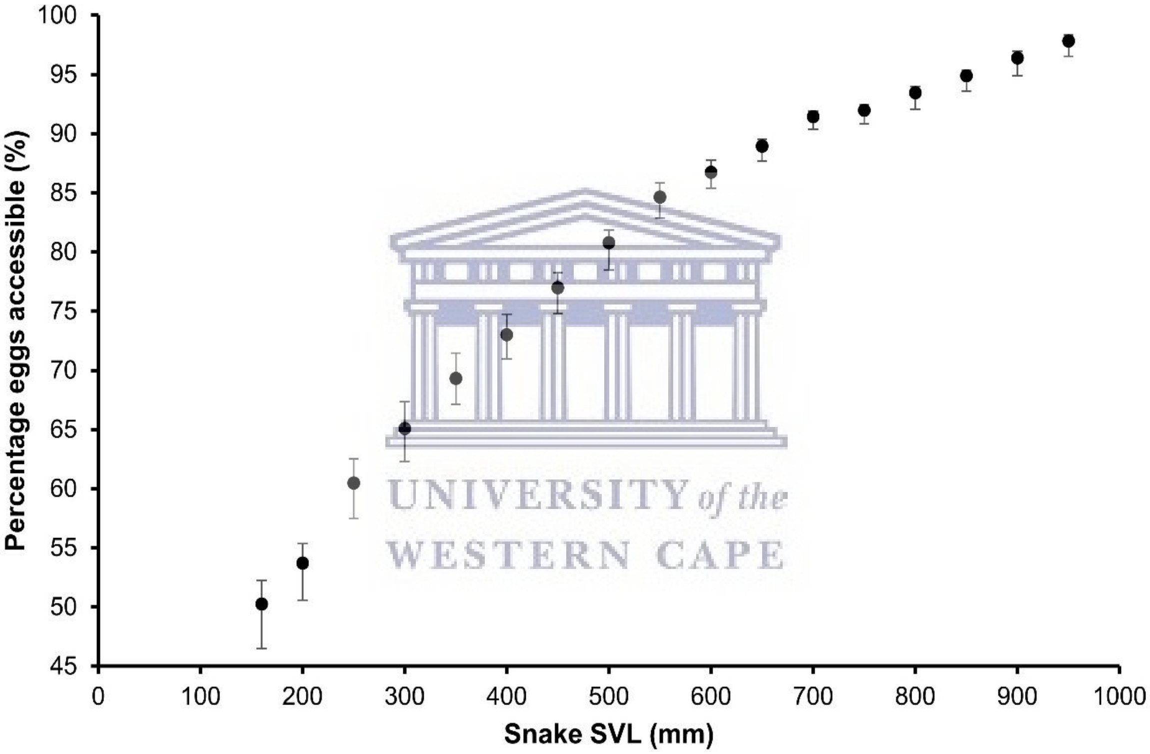

Fig. 4.2: Estimated average percentages of bird eggs accessible for consumption by different size classes of *Dasypeltis scabra* across southern Africa. Percentages are based on the maximum ingestion ability of 14 captive individuals and the average diameters of bird eggs deposited per country. Error bars denote minimum and maximum percentages across southern African countries.

4.4.3 Temporal variation in bird egg availability

Bird breeding in southern Africa exhibited clear seasonality with significant monthly variation in the numbers of breeding species (Chi-square test: $\chi^2_{\mathrm{df}=11} = 799.328$, $P < 0.001$ Fig. 4.3). Bird breeding peaks in spring, primarily during October, decrease in summer and dramatically drops during winter (May to July) (Fig. 4.3). In addition, the sizes of the eggs deposited in each month across southern Africa differed statistically (One-way ANOVA test of log-egg diameter: $F_{11,\ 12892} = 80.612$, $P < 0.001$), with the general trend being that smaller-sized eggs are less frequently deposited during winter (Fig. 4.4).

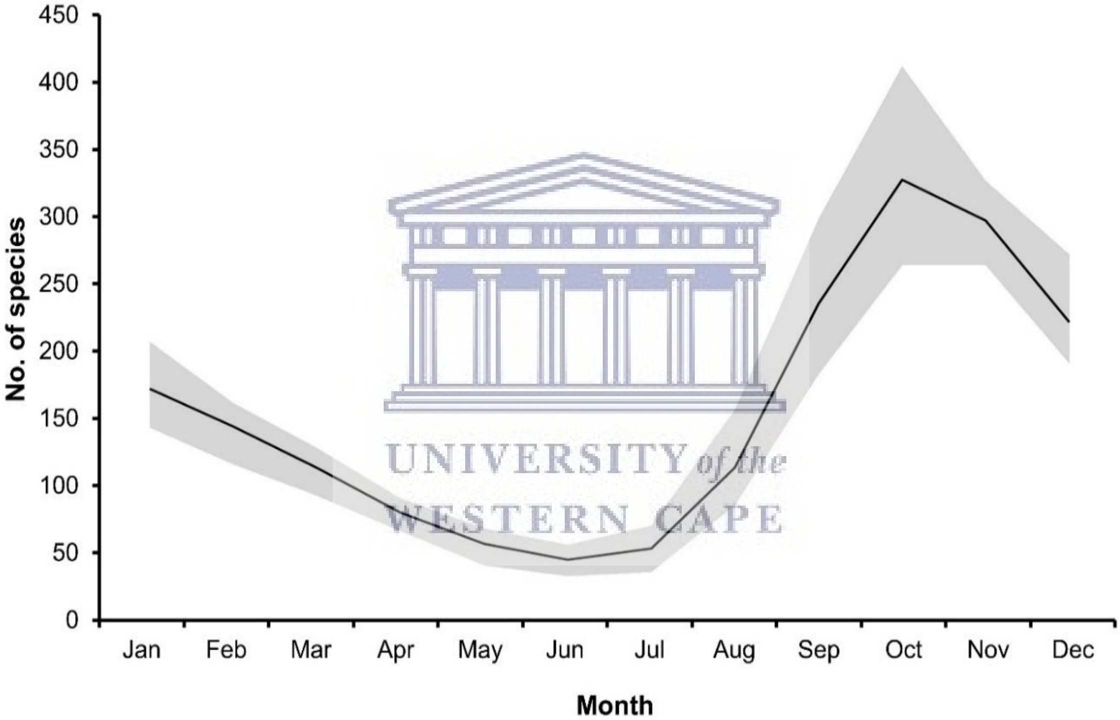

Fig. 4.3: Average numbers of bird species that deposit eggs during each month across southern Africa. The shaded area represents the minima and maxima across southern African countries.

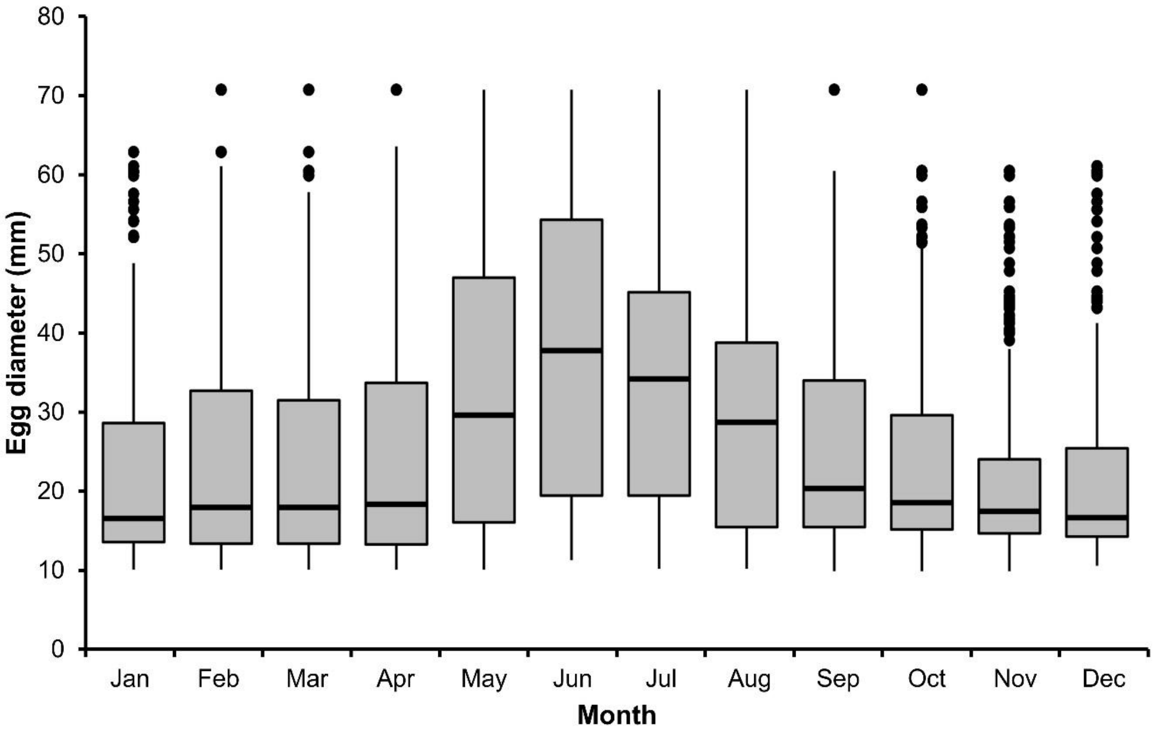

Fig. 4.4: Monthly variation in bird egg size distributions available across southern Africa. Black circles represent outliers.

4.5 Discussion

Dasypeltis scabra exhibits positive allometric scaling in the ability of individual snakes to ingest increasingly bulkier bird eggs. This scaling correlates with the number of bird species whose eggs can be consumed by snakes of differing size classes within a given region. I demonstrate that in southern Africa, adult *D. scabra* could feasibly consume the eggs of 98% of breeding bird species. Comparatively, roughly 50% of bird species' eggs are suitably sized for consumption by hatchling snakes. Importantly, while the upper limit of maximum ingestible egg size scales allometrically with increases in snake body length, the lower limit does not change as snakes grow —a pattern consistent with an ontogenetic telescope (Arnold 1993; Hamilton et al. 2012). This tendency for large snakes to accept small eggs when encountered likely arose as a result of the need to capitalize on feeding opportunities given the time-limited nature of bird egg availability. In southern Africa, bird breeding occurs year-round but peaks in spring and is greatly diminished during non-peak months. In particular, smaller bird eggs are less frequently available during colder months.

Predation of wild bird eggs by *Dasypeltis scabra* has been reported throughout the literature for several decades and the eggs of at least 40 species of birds are confirmed as prey of these snakes (Barends & Maritz 2022a). However, the number of bird species whose eggs are consumed by *D. scabra* is likely substantially higher given the abundant richness and diversity of sub-Saharan birds (Hockey et al. 2005). My results suggest that the eggs of 708 (of 728 breeding species, 98%) species of birds across southern Africa constitute suitably sized prey for large *D. scabra* in this region. This percentage matches the 98% estimated by Gartner & Greene (2008) for congeneric *D. atra*, although their analysis was restricted to only include ground-nesting birds (236 species). Prey resources for these snakes, therefore, appear to be abundant in space across this portion of *Dasypeltis*' range.

Despite reaching a maximum SVL of ~1000 mm, adult *Dasypeltis scabra* can ingest and consume nearly the entire range of available bird eggs. These snakes may thus have evolved towards an optimal maximum body size. Theoretically, individuals larger than 1000 mm would gain little advantage in terms of additional access to prey but would require more food to maintain body condition given their increased size. The unfavourable nature of this trade-off may have acted as a selective agent against larger body sizes for these snakes. Additionally, although its ecology is not well known, the Indian egg-eating snake (*Boiga westermanni*) appears to share many similarities to *Dasypeltis*, including bird egg specialization (Dandge 2008; Dandge & Tiple 2016) and a similar maximum body length of 800 mm SVL; Feldman et al. 2016), showing potential convergence towards an optimal size for obligate oophagous snakes.

Much attention has focused on the remarkable feats of ingestion performed by large *Dasypeltis* (Gans 1952; Broadley 1990; Gartner & Greene 2008; Bates & Little 2013) but the ingestion ability and corresponding foraging habits of juvenile snakes have largely been subject to speculation. Bates (1990) estimated that juvenile *Dasypeltis* of 210 – 240 mm in SVL could feasibly consume eggs as wide as 17.4 mm, and suggested that the eggs of various species of cisticolas and larks were likely to be their primary source of prey. Bates & Little (2013) further hypothesized that the eggs of various prinias, quails, warblers, waxbills, weavers, and widow-birds are also likely candidates. My results indicate that a considerably wider selection of bird eggs is suitably sized as potential prey for juvenile snakes than previously thought. In the laboratory, newly hatched neonates (< 200 mm SVL) ate eggs as wide as 15.4 mm in diameter and are estimated to be capable of consuming eggs up to 17.94 mm. Accordingly, the eggs of 363 species of southern African birds (50% of species) constitute suitable prey for small *D. scabra* —a substantially greater number of species than previously estimated. Moreover, since I cannot rule out that snakes might have refused some larger eggs for reasons other than gape limitations (for example egg quality, fluctuations in ambient temperature, scent interference etc.), the slope of my regression equation may have been restricted to some extent. In reality, juvenile snakes could be capable of consuming slightly larger eggs, and thus slightly more species, than is evident in this study.

The *Dasypeltis scabra* individuals in my study exhibited a feeding pattern typical of an ontogenetic telescope in prey size preferences. Adult snakes consumed considerably bulkier eggs than juveniles but also ate small eggs when these were offered. The tendency for *D. scabra* to continue to consume small eggs as they grow could be due to several reasons. Firstly, despite their size, even small bird eggs provide relatively high quantities of proteins, lipids, water, and caloric content (Menezes & Marini 2017). Consuming even small eggs is thus likely to be energetically profitable, especially as these snakes are known to sometimes consume entire clutches in single sittings (Lloyd et al. 2001; Lloyd 2004; Bates & Little 2013). Secondly, smaller eggs are probably easier to consume than bulkier eggs as the shells are more fragile and easier to breach which could reduce handling time. In the laboratory, snakes typically took between ~20 minutes and ~1 hour to ingest and breach large eggs. Reduced handling time could be desirable when foraging, especially given the risks associated with raiding nests (for example Bruderer 1991) as well as other extrinsic factors like competition. Moreover, the ephemeral, time-limited nature of bird egg availability means that *Dasypeltis* must capitalize on feeding opportunities when eggs are encountered and so snakes are unlikely to pass up ingestible meals of any size.

The temporal constraints on prey availability associated with seasonal bird breeding appear to limit the feeding opportunities of *Dasypeltis scabra* in most regions. However, these constraints do not appear to preclude the obligate specialization of bird eggs across different size classes of snakes. My results show that in southern Africa, bird egg availability is greatly reduced for much of the year because few species of birds breed in autumn and winter, resulting in restricted foraging opportunities for *D. scabra* during these months. In particular, smaller-sized eggs are extremely limited outside of the peak breeding months making foraging at those times extremely difficult for juvenile snakes. However, Greene et al. (2013) showed that *D. scabra* have low standard metabolic rates (SMR) and reduced metabolic expenditure compared to other members of the family Colubridae and were more similar to infrequent feeding, ambush foraging snakes of the Boidae, Pythonidae, and Viperidae families. In addition, Greene et al. (2013) found that neonate *D. scabra* has remarkably low mass-specific SMR even compared to larger individuals of the species. Given that neonates usually hatch in February/March (Alexander & Marais 2007), young snakes are unlikely to feed for the first few months of their lives. The low SMR of *D. scabra*, particularly juveniles, is thus likely to have developed as a result of selective pressures caused by prolonged periods of restricted food availability. Rather than consume other prey, *D. scabra* has seemingly evolved to withstand extended periods of food shortages.

The ability of individual *Dasypeltis scabra* to fast for several months has important implications for their circannual activity patterns. The combination of reduced prey during winter with declines in temperature means that foraging during these months is unlikely to be energetically profitable. Instead, *D. scabra* tends to undergo winter brumation (Broadley 1990; Branch 1998; Bates & Little 2013). When egg-laying peaks, generally in October, snakes then maximize their feeding opportunities by rapidly predating eggs as they become available. *Dasypeltis*, therefore, tend to show seasonal patterns in their detection probability and circannual rhythms that coincide with peaks in bird breeding. The above claims are somewhat supported by monthly variation in *ad hoc* observations of wild *D. scabra* shared on the community science platform iNaturalist (Fig. S4.2).

While *Dasypeltis* can seemingly withstand long periods without feeding every year, they are likely to be limited in the extent to which they can fast. In some environments where bird breeding is rainfall dependent but rainfall is unpredictable and may skip seasons (Lloyd 1999; Cox et al. 2013), the unpredictable nature of the availability of eggs may exceed the limits of the fasting ability of *Dasypeltis* and thus may exclude them. This could explain why these snakes appear to be absent in some parts of their range such as in the Kalahari (Bates et al. 2014). Moreover, this could also explain why their distribution does not extend into the Sahara.

Several aspects of the foraging ecology of *Dasypeltis scabra* and their prey remain open for further investigation and could provide additional insight into the evolution of dietary specialization within these snakes and other taxa. While a plethora of bird eggs are available as prey for egg-eaters year-round, it remains unclear how many eggs are consumed by the average individual per annum. Additional investigations could seek to quantify the food intake requirements of different age classes of *D. scabra* needed to maintain body condition, grow, and reproduce. Similarly, investigations into the densities and population sizes of *D. scabra* and their prey could provide valuable insight into understanding food constraints and potential competition dynamics within this species of snakes. Further insights into these topics could build upon my findings and may provide a deeper understanding of how ecological specialists have evolved, and continue to persist.

4.6 Acknowledgements

Animals used in this study were collected under the following permits: Cape Nature CN44-31-11003 and CN44-87-17733. Ethical clearance for this study was approved by the Animal Research Ethics Committee of the University of the Western Cape: AR 20/1/2. I thank Robin Maritz for assisting with snake feeding and data collection. I thank Kim Scholtz for assisting with snake welfare. This work was funded by the National Research Foundation: UIDs 118090, 123281, and 139202.

Chapter 5: Circannual Feeding and Growth Patterns of *Dasypeltis scabra*

5.1 Abstract

Food supply and demand are important ecological processes that affect many biological processes of organisms, including their growth and fitness. I measured annual food intake and growth rates in a colony of captive African egg-eating snakes, *Dasypeltis scabra* over three years. My results show that the growth rate of snakes was not related to body size. Under the thermal regime experienced by the colony of snakes, they required food equal to an average of only 61% initial body mass to maintain body condition over a period of 12 months. Moreover, individuals exhibited a seasonal feeding rhythm as food acceptance was highest during spring and summer months (October to February) coinciding with peaks in bird egg-laying habits. In addition, ecdysis frequency occurred in concert with appetite and was highest following periods of high food acceptance. I interpret these results to suggest that appetite and ecdysis in *D. scabra* are endogenously controlled. I argue that seasonal breeding by southern African birds was likely the selective force that led to the low food maintenance requirements and seasonal feeding patterns in *D. scabra*.

5.2 Introduction

All animals have food requirements they must meet to survive, grow, and reproduce (Schoener 1977; Madsen & Shine 2002; McCue 2010). Food supply and demand are therefore important selective forces of organismal evolution and ecology. As ectotherms, snakes can endure prolonged periods without feeding (Greene 1997; McCue 2007). Accordingly, several snake species have evolved low maintenance metabolic rates that allow them to undergo extended periods of starvation and concomitant digestive quiescence (Secor & Diamond 1998; Christian et al. 2007; McCue 2007; Greene et al. 2013). Moreover, many snakes can consume considerably large meals relative to themselves (Arnold 1993; Greene 1997), including meals exceeding their own body mass (Shine 1991a; Wiseman et al. 2019), that provide substantial energetic gains. As a result, many species of snakes can subsist on only a few large meals per year if required, provided that those meals are sufficiently rich in energy.

Food intake rates of snakes can determine several biological and ecological aspects of their life histories. For example, food intake is generally positively related to growth (Alexander 1996; Bonnet et al. 2001b; Madsen & Shine 2002), can affect organ regulation (Wang & Rindom 2021), digestion (Secor 2008), reproductive performance (Bonnet et al. 2001a), and can influence spatial movement (Glaudas & Alexander 2017). Understanding snake appetite can therefore provide important insight into their ecologies and ecological roles as predators. Generally, snake appetite, and thus growth, is affected by several factors including, but not limited to, fluctuations in prey abundance and availability (Madsen & Shine 2000; Brown et al. 2017), or shifts in temperature and other environmental changes (Webber et al. 2016). However, an increasing body of evidence shows that in some cases, feeding and growth may be intrinsically driven by endogenous processes (Blem & Kileen 1993; Alexander & Brooks 1999; Lamonica et al. 2007).

The rhombic egg-eater, *Dasypeltis scabra*, is an important predator in African ecosystems. Widespread throughout much of east and southern Africa (Bates et al. 2014; Bates & Broadley 2018), *D. scabra* (and other *Dasypeltis* throughout sub-Saharan Africa) obligately feed on bird eggs and consume no other types of prey (Gans 1952; Bates & Little 2013). Many species of birds act as important ecosystem engineers by contributing to landscape-altering processes like seed dispersal, pollination, and nest construction (Whelan et al. 2015; Floyd & Martin 2016). Thus, the modulation of recruitment on bird populations, through nest predation by *D. scabra* could indirectly affect a host of organisms and ecological processes.

Research from recent decades (e.g. Lloyd et al. 2001; Lloyd 2004; Nalwanga et al. 2004; Lloyd et al. 2009; Underhill et al. 2012) suggests that predation by *Dasypeltis scabra* is the leading cause of nest failure among southern African bird species. However, the extent to which these snakes impact bird recruitment is still largely unclear. Surprisingly little is known about the feeding habits of wild *D. scabra* beyond broad generalizations made from our knowledge of their feeding mechanics. *Dasypeltis scabra* has evolved a near-globally unique approach to oophagy in which snakes generally only consume the liquid contents of eggs and regurgitate the shells (Gans 1952 Gans 1974, but see Barends et al. 2021). By only consuming the liquid contents of eggs, these snakes can purportedly consume multiple eggs per sitting with ease (Gartner & Greene 2008; Greene et al. 2013) and can thus consume entire clutches from nests. However, direct observations of wild snakes feeding are rare (Bates & Little 2013; Barends & Maritz 2022a) and food intake rates of individuals are unclear, making it difficult to quantify the impact of *Dasypeltis* predation on bird breeding.

Here, I quantified the annual food intake and growth rates of a colony of 13 *D. scabra* in a laboratory for three years. Given that bird eggs are a rich source of calories, protein, lipids, and water (Sotherland & Rahn 1987), I hypothesize that individual *D. scabra* only requires a few egg meals to sustain themselves and grow each year. To test this, I estimate the annual minimum feeding requirements of these snakes by comparing the quantity of food that snakes required (as a percentage of body mass) to maintain initial body mass for 12-month periods. Moreover, since bird breeding in southern Africa is seasonal, I hypothesize that snake appetite is likely to show synchrony with seasonal fluctuations in bird egg availability. Accordingly, I tested if snakes feed more frequently in warmer months when eggs are available and fast during colder months when eggs are absent. Since feeding is often related to growth, I also quantified monthly variation in snake ecdysis probability. Lastly, I discuss the potential impact of *D. scabra* on bird recruitment and ecosystem functioning.

5.3 Methods

5.3.1 Snake husbandry and data collection

I housed a colony of 13 wild-caught *Dasypeltis scabra* specimens from Cape Town, South Africa for three years from January 2019 to December 2021. The colony comprised a mixture of adults and juveniles ranging in initial capture mass from 3.4 – 244 g (average = 35 g). Snakes were housed individually in plastic enclosures (260 x 350 x 120 mm for juveniles or 420 x 600 x 200 mm for adults) in a windowed laboratory under natural light at the University of the Western Cape. Ambient temperature in the laboratory ranged from 15.2 – 25.6°C for the duration of the study.

Snakes were maintained on assorted bird eggs of varying sizes obtained from local breeders. These predominantly consisted of the eggs of zebra finches (*Taeniopygia guttata*), rock pigeons (*Columba livia*), coturnix quails (*Coturnix coturnix*), and domestic chickens (*Gallus domesticus*). I weighed all snakes and their egg meals (to the nearest 0.01 g) immediately before feeding. I offered snakes monthly egg meals consisting of between one and three eggs depending on egg availability. To minimise the impact of my presence on food acceptance, I placed eggs in each individual’s enclosure and left them to feed. Uneaten eggs were removed from enclosures after seven days. Following the consumption of eggs, I also weighed the regurgitated eggshell remains to establish the mass of the consumed liquid content of each egg. For each snake, I recorded the numbers and mass of eggs offered, accepted, and rejected. I also recorded the dates of all ecdysis events over the three-year study period.

5.3.2 Feeding and growth

I evaluated the relationship between food intake and snake growth via ordinary least squares regression analyses. I tested the hypothesis that annual growth rate was positively correlated with relative food mass intake and that the intercept (which denotes maintenance intake, Alexander 1996) would be low relative to other snakes in which this has been measured. To do this, I regressed the relative growth of each snake against its relative food intake over a single year to calculate the food required by snakes to exhibit no change in growth for this period. I calculated relative growth as the change in body mass over one year divided by the initial mass of the snake at the start of the year. I calculated relative food intake as the total mass of food consumed (summed egg mass minus summed regurgitated egg shells mass) within a year divided by body mass at the start of the year. I only included data for snakes that were maintained for entire years and so sample sizes for each year vary as snakes were added to or removed from the colony.

I performed ordinary least squares regressions for each year individually, as well as averaged over all three years (i.e. the sum of each snake’s relative growth over each year/number of years versus the sum of each snake’s relative food intake over each year/number of years). I also performed a regression on pooled data of each respective year (i.e. all data from 2019, 2020, and 2021) collectively in a single analysis. Using the regression equations from the above regressions, I then estimated the minimum annual food requirements of snakes to maintain body condition by calculating the value of the x-intercept (i.e. relative food intake) where y (relative growth) equals 0 (i.e. no change in growth). Following the methods of Alexander (1996), I also tested if snake growth was independent of snake sizes by regressing the residuals of the previous regression analyses against the body mass of each snake.

5.3.3 Feeding and seasonality

Following Alexander & Brooks (1999), I calculated monthly food acceptance rates by quantifying the percentage of offered eggs that were consumed by each snake. I then binned these percentages per month and averaged them across all individuals to calculate the mean monthly acceptance rates. I applied an arcsine transformation to these measures before comparing monthly variation of food acceptance over the three-year study period using a repeated-measures ANOVA. Specific monthly differences were calculated *post hoc* via Bonferroni pairwise comparisons.

5.3.4 Ecdysis frequency

I calculated monthly ecdysis probabilities by dividing all recorded ecdysis events by the total number of snakes in the colony each month. I then used a repeated-measures ANOVA to compare arcsine-transformed monthly proportions of ecdysis over the three-year study period. I again assessed month-on-month differences *post hoc* via Bonferroni pairwise comparisons. Lastly, I used regression analyses to assess the relationship between feeding and ecdysis. For this analysis, I compared average monthly food acceptance rates to monthly ecdysis probabilities over three years.

5.4 Results

5.4.1 Feeding and growth

Snakes consumed an average of 3.703 eggs per year (standard deviation = 2.379, total eggs consumed = 137). Regression analysis revealed a positive linear relationship between annual food consumption and growth relative to snake body mass averaged over three years ($F_{1,11}$ = 103.958, $P < 0.001$, $R^2 = 0.90$; Fig. 5.1). This pattern was consistent when assessing each year individually and when data for all three years were pooled together (Table 5.1). On average, snakes met annual maintenance requirements by consuming 61% (inter-annual variation: 56 – 71%) of their initial body mass at the beginning of that year (Fig. 5.1). Additionally, I found no association between the residuals of the above regressions and the respective body masses of snakes (Table 5.1), indicating that growth relative to snake size was independent of initial snake size.

Table 5.1: Results of regression analyses comparing relative feeding and relative growth of *Dasypeltis scabra*.

Comparison	F	P	R^2	n	Yearly maintenance food required (%)
Growth / food intake (2019)	26.547	< 0.001	0.791	9	55.95
Growth / food intake (2020)	31.705	< 0.001	0.742	13	71.11
Growth / food intake (2021)	31.984	< 0.001	0.820	9	70.68
Growth / food intake (averaged)	103.958	< 0.001	0.904	13	60.57
Growth / food intake (pooled)	149.760	< 0.001	0.836	31	62.31
Residuals / body mass (2019)	4.047	0.084	0.366	9	-
Residuals / body mass (2020)	0.072	0.793	0.007	13	-
Residuals / body mass (2021)	0.015	0.907	0.002	9	-
Residuals / body mass (averaged)	0.577	0.463	0.049	13	-
Residuals / body mass (pooled)	0.180	0.674	0.006	31	-

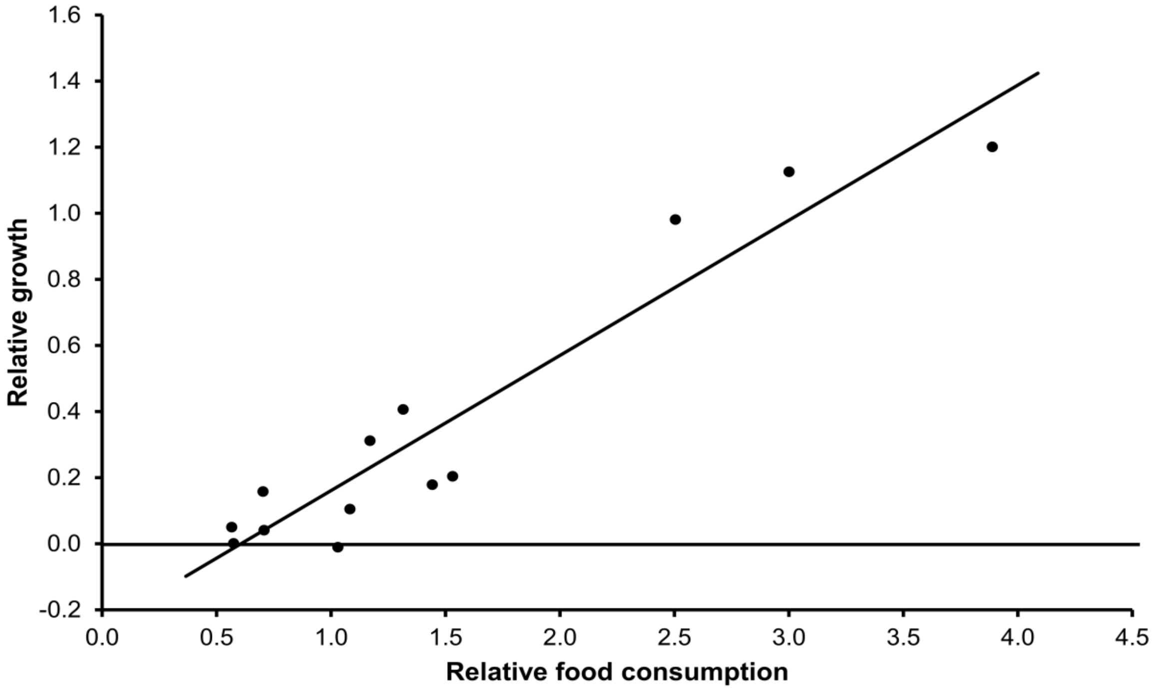

Fig. 5.1: Annual relative food consumption and relative growth of 13 *Dasypeltis scabra* averaged over three years (2019 – 2021). Linear regression equation: $y = a + bx$: a = -0.2476, b = 0.4089, $R^2 = 0.90$, $P < 0.001$. The point at the x-intercept where y = 0 indicates the minimum annual food required to maintain body mass.

5.4.2 Feeding and seasonality

Rates of food acceptance significantly differed between months (Repeated measures ANOVA: $F_{11, 1} = 7.379$, $P = 0.020$; Fig. 5.2) but not between years ($F_{2, 10} = 1.347$, $P = 0.303$). Monthly variation in food acceptance was therefore consistent across the three years. Of 66 Bonferroni pairwise comparisons between monthly pairs, 13 pairs differed significantly (Table S5.1). These differences occurred between late-spring and summer months (October to February) where acceptance was high (average food acceptance = 49.90%, min = 39.41, max = 78.34%) and winter months (May to August) where acceptance was minimal (average food acceptance = 5.01%, min = 0.00%, max = 13.33%).

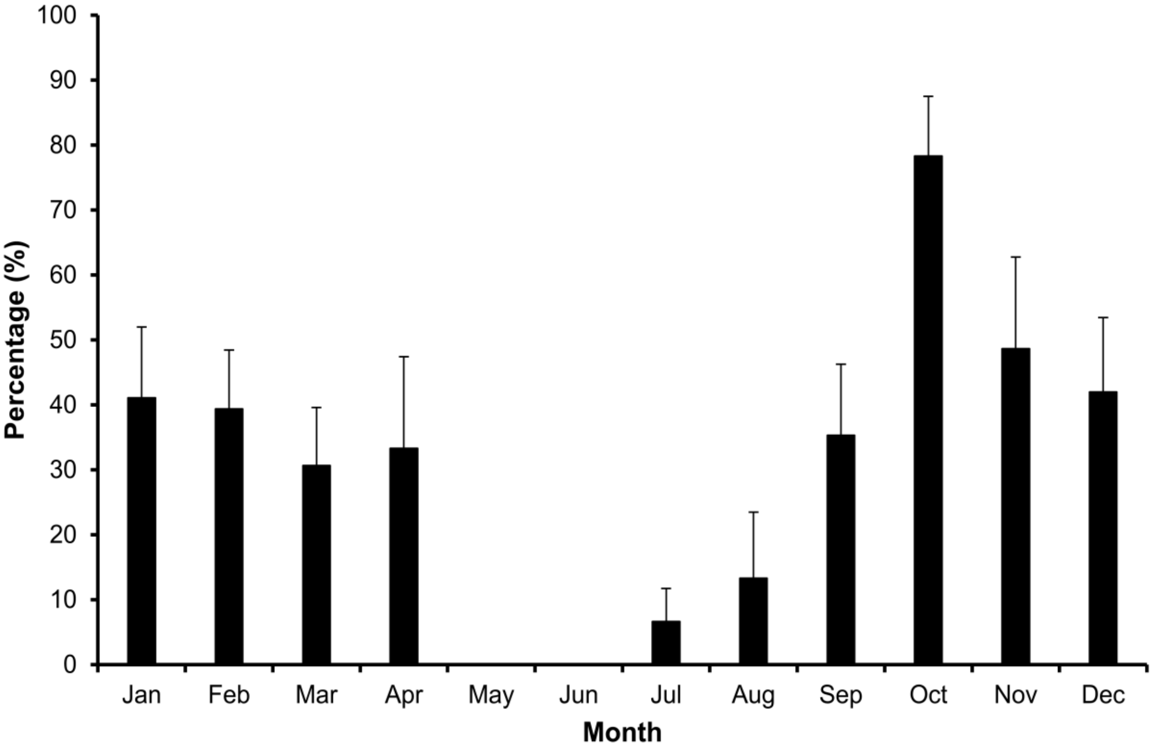

Fig. 5.2: Average monthly food acceptance of 13 captive *Dasypeltis scabra*. Data were collected from 2019 through 2021. Error bars denote standard error.

5.4.3 Ecdysis frequency

On average, individuals shed 1.03 times per year (standard deviation = 0.48; total number of sheds = 54). Repeated measures ANOVA revealed that the probability of ecdysis events differed significantly between months ($F_{11,1} = 4.815$, $P < 0.001$; Fig. 5.3) but not between years ($F_{2, 10} = 2.590$, $P = 0.124$). Of 66 monthly Bonferroni pairwise comparisons, eight pairs significantly differed (Table S5.2). Ecdysis most frequently occurred during summer months between December and February (average = 0.20, min = 0.16, max = 0.23) before decreasing substantially during March and April (average = 0.06, min = 0.06, max = 0.07). No ecdysis events were recorded between May and August.

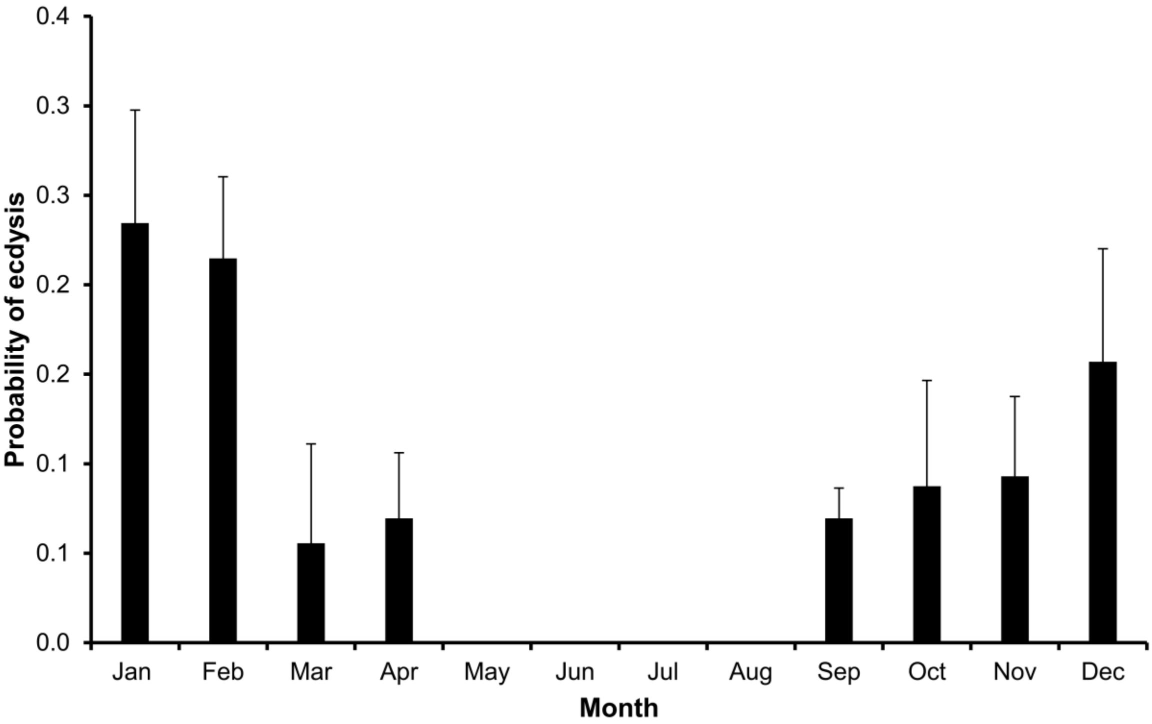

Fig. 5.3: Average monthly probabilities of ecdysis of 13 captive *Dasypeltis scabra*. Data were collected from 2019 through 2021. Error bars denote standard error.

5.5 Discussion

Food intake and growth in *Dasypeltis scabra* showed a strong positive relationship that was independent of body size and exhibited clear seasonality. Snakes required an average minimum food intake equal to 61% initial body mass per annum to remain at constant body mass. Appetite and ecdysis frequency were highest in spring and summer months respectively and lowest in winter months, mirroring expected patterns of bird egg abundances. These results suggest that external factors of food availability likely shaped the circannual feeding and growth patterns in *D. scabra*.

Annual food intake was significantly related to relative growth rates in the colony of *Dasypeltis scabra*. Unsurprisingly, snakes that consumed the most eggs each year showed greater increases in body mass than those that only ate a few eggs. Importantly, relative growth rates were independent of snake body size, and therefore likely snake age. This indicates that juveniles and adults likely do not have inherently different growth capacities and suggests that food intake rather than genetic factors are the primary determinants of growth for these snakes. Similar trends have been observed in other snake species (Alexander 1996; Madsen & Shine 2000). However, for other species, physiological factors like sexual size dimorphism are also known to affect growth rates (Brown & Weatherhead 1999). I did not explicitly test for the effects of sex or other factors on snake growth and thus cannot rule out that they may have influenced growth in *D. scabra*. Regardless, my data suggest that growth in *D. scabra* is largely dependent on feeding and thus prey availability.

The *Dasypeltis scabra* in the colony required an average of just 61% body mass of food to maintain body condition annually under captive conditions. This estimate was likely affected by the limited energy expenditure resulting from snakes living in captivity and is probably higher for free-ranging snakes that must expend energy on foraging and other activities (Beck 1995). However, the yearly food requirements of the colony of snakes were substantially lower than for other colubrid species like *Diadophis punctatus* (125%; Schoener 1977), *Thamnophis sirtalis* and *T. radix* (300 – 400%; Reichenbach & Dalrymple 1986), vipers like *Agkistrodon contortix* (300%, Schoener 1977), or elapids like *Hemachatus haemachatus* (71% when fed mice, 131% when fed frogs, Alexander 1996) kept under captive conditions. The annual maintenance requirements of *D. scabra*, therefore, appear to be exceptionally low compared to other snakes.

The low maintenance requirements of *Dasypeltis scabra* could be partially explained by seasonal variation in food consumption. In southern Africa, bird breeding shows distinct seasonality with breeding being high during the austral spring and summer, peaking in October, before rapidly decreasing in winter (Tarboton 2011). The snakes in the colony most frequently fed in late spring and summer months and seldomly ate in winter, matching the above pattern despite food being offered in all months. This suggests that appetite in at least the colony of *D. scabra* is likely endogenously controlled with snakes following a circannual rhythm to feed in months when eggs are abundant and fast during months when eggs are less frequently available. Thus, these snakes likely developed low metabolic rates in response to prolonged periods without food during colder seasons.

Causal factors not directly related to appetite may have influenced the observed monthly trends in food acceptance. Because I did not keep environmental conditions constant throughout my study, snakes may have refused to eat on occasion because of fluctuations in environmental cues that can affect snake feeding such as temperature (Alexander & Brooks 1999). I therefore cannot rule out that monthly variation in food acceptance was not exclusively driven by snake appetite. However, given that monthly shifts in appetite did not directly correlate with monthly shifts in temperature (e.g. acceptance rates were highest in spring rather than warmer summer months, and lowest in May rather than colder winter months), the effects of temperature are likely to have only minimally affected snake feeding.

Other factors unrelated to environmental feeding cues could additionally have limited food acceptance rates. *Dasypeltis* purportedly prefer freshly laid eggs (Branch 1998; Bates & Little 2013; Greene et al. 2013) and wild snakes have a remarkable propensity to find and consume newly laid eggs as they become available (for example Jacobsen 1989). Although I took care to ensure the preservation and freshness of eggs, food acceptance rates could have been affected by the quality of eggs offered. Additionally, physiological factors like ecdysis can also affect feeding. In general, appetite decreases leading up to ecdysis events, especially during the opaque phase when activity levels are wholesale reduced (King & Turmo 1997; Alexander & Brooks 1999; Lamonica et al. 2007). Given that the snakes most frequently shed in summer, this may have potentially limited the peaks in food acceptance during those months.

Probabilities of ecdysis among snakes were highest in summer, peaking in January, before significantly decreasing through winter months. Peaks in ecdysis thus appeared to occur following months with high rates of food acceptance. However, these trends do not necessarily mean that high food intake is causal to subsequent shedding. Snake shedding is generally (Lillywhite 2014), but not always (Alexander & Brooks 1999; Lamonica et al. 2007), related to growth and usually follows pronounced periods of feeding, which tend to be more prevalent in summer. However, many species shed most frequently in summer regardless of food intake because high temperatures and humidity facilitate the shedding process and decrease the risk of problems relating to cellular growth (Lillywhite & Sheehy 2016). Ecdysis in *Dasypeltis scabra* could therefore primarily occur in summer for several reasons, including, rapid growth following gluttonous spring feeding, the unfavorability of shedding and concomitant fasting during periods of high food availability in spring, and favourable environmental conditions of summer.

Dasypeltis scabra is considered the primary predatory threat to the eggs of nesting birds in southern Africa (Lloyd et al. 2001; Nalwanga et al. 2004; Lloyd et al. 2009; Bates & Little 2013). At least 40 species of bird eggs are known prey of these snakes (Bates & Little 2013; Maritz & Maritz 2020; Barends & Maritz 2022a) but their diet likely includes several more species. Greene et al. (2013) speculate that a 50 g adult could conceivably consume the contents of between 25 and 50 nests each containing four eggs (~1 – 3 g respectively) in a single season. This would represent a relative food intake of 100 – 1200% of initial body mass. The highest percentage of food intake relative to the initial mass of an individual snake in the colony here over any single year was 539%, which falls within the above range. However, this individual achieved this by consuming just seven eggs, considerably less than the estimated 100 – 200 eggs required for the above scenario. Moreover, no individual snakes consumed more than nine eggs in any single year. My results, therefore, suggest that egg size rather than egg quantity drives feeding in *D. scabra*.

Since I did not feed snakes *ad libitum*, my results do not allow me to estimate the upper limits of *Dasypeltis scabra* appetite. Regardless, I contend that the average individual is unlikely to consume much more than one or two dozen eggs per year. The combination of seasonal shifts in temperature and prey abundances coupled with monthly variation in appetite limits feeding opportunities to a window of only a few months during peak bird egg-laying periods. Individuals are assumed to feed rapidly during this time to maximize their food intake and build up fat reserves (Bates & Little 2013). However, snakes are unlikely to feed continuously without allowing time for meals to digest and assimilate. For modestly sized meals of 20% body mass this could take up to two weeks (Greene et al. 2013), and likely takes longer for larger meals. *Dasypeltis* therefore cannot forage for the entirety of the peak laying period. In addition, bird eggs are ephemeral in their availability and do not remain as eggs for extended periods. In southern Africa, the mean incubation time across all bird species is approximately 20 days (Tarboton 2011). It thus appears unlikely that a single snake would attack more than a handful of nests within a single season. An investigation of *Dasypeltis* activity through radio telemetry or other techniques could provide further insight into their foraging behaviour.

Reports of intensive predation by *Dasypeltis scabra* on bird populations have been documented in a few cases (for example Lloyd et al. 2001; Lloyd 2004; Pryke & Lawes 2004; Bates & Little 2013). Given the findings of my results here, I speculate that in those cases, *D. scabra* is likely to have been present in those areas at high abundances and that the high rates of predation were a result of several snakes feeding. To effectively evaluate how *Dasypeltis* contribute to ecosystem functioning, both directly and indirectly, future studies should seek to build on the results here, and elsewhere (for example Gartner & Greene 2008; Greene et al. 2013), in conjunction with estimates of snake population abundances.

5.6 Acknowledgements

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Chapter 6: An Estimate of *Dasypeltis scabra* Population Density at Koeberg Private Nature Reserve

6.1 Abstract

Predators are essential components of ecosystems and estimates of predator abundance and population density are critical for understanding ecosystem functioning. However, these measures can be difficult to obtain when species have low detectability. Consequently, the population ecology of many cryptic predators like most species of snakes is unknown, often leading to these species being perceived as rare and thus of little functional importance. Here, I estimated the population density of the obligate, bird egg specialist rhombic egg-eater, *Dasypeltis scabra* at Koeberg Private Nature Reserve (~2900 ha) along the west coast of Cape Town, South Africa. I used arrays of artificial cover objects with known locations to capture and mark snakes between August 2020 and April 2022. I fitted four spatially-explicit capture-recapture models on snake capture data at two sites of different vegetation types (Fynbos and Strandveld respectively). Model performance was compared using Akaike information criterion scores corrected for small sample sizes (AICc). Population density estimates of the best performing models of each site were high (5.79 ha^{-1} and 8.28 snakes ha^{-1} respectively). By process of extrapolation, Koeberg Private Nature Reserve may thus be occupied by > 14 000 individuals. Should each of these individuals consume the minimum annual requirement of ~3 bird eggs per year, this translates to an excess of 40 000 eggs that are removed by predation from *Dasypeltis scabra* each year. These estimates highlight the functional importance of snakes as predators by modulating prey in large numbers, emphasizing the need to critically evaluate their functional roles and ecological importance.

6.2 Introduction

In recent decades, research in the field of functional ecology has highlighted the importance of predators in sustaining ecosystem functioning (Ripple et al. 2014; Sergio et al. 2014; Mattioli et al. 2018). Through top-down trophic interactions, predators directly impact the population structure of their prey (Estes et al. 2011). Moreover, these impacts can indirectly contribute to maintaining biodiversity by regulating vital ecosystem processes like energy transfer and nutrient cycling (Hooper et al. 2005; Gascon et al. 2015). Accordingly, obtaining estimates of predator population sizes is an important component of ecosystem management. Unfortunately, many predators are elusive (Witmer 2005), making it difficult to acquire the necessary data to perform robust calculations of their abundance and population densities.

Snakes represent a group of ~4000 species (Uetz et al. 2021) of predators that are highly cryptic, elusive, and have remarkably low detectability (Durso et al. 2011). As a result, except for a few well-studied communities in the northern hemisphere, population estimates of snakes are incredibly scarce across the globe (Parker & Plummer 1987; Mullin & Siegel 2009). Consequently, even in areas with high snake species richness, most species of snakes are perceived to be rare and thus of negligible ecological importance (Willson & Winne 2016).

The notion that snakes are rare and thus ecologically unimportant is almost certainly untrue. Snakes occur throughout the globe on all continents except Antarctica and are present in nearly every type of habitat (Greene 1997). Estimates of snake density from North America suggest some species can occur at incredibly high densities > 1200 snakes ha^{-1} (Fitch 1975; Godley 1980) and could thus be responsible for high rates of predation. Recent examples from island populations and invasive species in Guam and Florida respectively (Rodda et al 1992; Dove et al. 2012) highlight the impact of snake predation as a top-down regulator of prey population numbers. Unfortunately, similar results have yet to be observed in most parts of the globe in native systems, in large part due to a lack of research on snake population ecology.

The lack of snake population studies in some parts of the globe can be attributed to several factors. Firstly, the unique biology and elusive behaviour of most snakes make it challenging to acquire the quantitative data required for mark-recapture or occupancy analyses (Mazerolle et al. 2007; Muñoz et al. 2016). Secondly, sampling in some areas may be problematic because those areas are difficult to access or reside in politically unstable regions, making it logistically challenging to perform fieldwork (Maritz & Alexander 2012; Tolley et al. 2016). Thirdly, different sampling approaches vary in their costs, with some methods requiring expensive and often unaffordable equipment like PIT tags and radio-telemeters (Leuenberger et al. 2019). Nevertheless, a variety of practical and relatively inexpensive field techniques are available for capturing snakes (for example pitfall traps, funnel traps, artificial cover objects, etc.) which can be used with a myriad of statistical models to estimate population metrics.

Here, I present estimates of population density for a widespread, obligate bird egg specialist snake, the rhombic egg-eater (*Dasypeltis scabra*) using a spatially-explicit capture-recapture (SECR) approach. SECR models use a combination of location and capture history data of captured individuals to calculate population density (D), capture probability ($g0$) and the spatial scale of detection (σ) (Efford 2018). I used artificial cover objects to capture snakes at known locations at three sites within Koeberg Private Nature Reserve in Cape, Town, South Africa. Specifically, my objectives were to estimate *D. scabra* population density at each site and compare estimates between sites to calculate the potential number of individuals within the reserve.

6.3 Methods

6.3.1 Study species

Dasypeltis scabra is a species of widespread colubrid snake that occurs throughout much of sub-Saharan Africa. Their range extends from Cape Town, South Africa northwards through the Democratic Republic of Congo, and eastwards through Ethiopia and South Sudan (Bates et al. 2014; Bates & Broadley 2018; Spawls et al. 2018). These snakes inhabit several habitat types including fynbos, grasslands, savannas, scrublands, and semi-arid areas (Bates et al. 2014) where they obligately feed on various bird eggs (Branch 1998; Bates & Little 2013). Given their large geographic range, apparent abundance, and specialized diets, these snakes are considered the primary predatory threat to avian nesting success in sub-Saharan African systems (Bates & Little 2013; Bates & Broadley 2018).

6.3.2 Study site

This study was conducted at Koeberg Private Nature Reserve (KNR), situated on the west coast of South Africa (33° 40’ S, 18° 26’ E, 10 m above sea level) (Fig. 6.1). This reserve is privately owned by Eskom and covers an area of approximately 2900 ha (Le Roux 2014). KNR has a Mediterranean climate and experiences cold, rainy winters and hot, dry summers (Rohwer et al. 2017). Winter temperatures in the reserve average 17°C and summer temperatures average 28°C (Rohwer et al. 2017). Mean annual rainfall in the reserve is 375 mm (Lloyd et al. 2014). KNR is dominated by two vegetation types: Cape Flats Dune Strandveld vegetation consisting of dense, medium-sized (< 2m) shrubs, and Atlantis Sand Fynbos vegetation consisting of smaller, more isolated shrubs (Mucina & Rutherford 2006). At least 11 species of snakes occur at KNR (Bates et al. 2014), including oophagous boomslang (*Dispholidus typus*), Cape cobras (*Naja nivea*), rhombic egg-eaters (*Dasypeltis scabra*), and mole snakes (*Pseudaspis cana*). Other snakes in the reserve include

Crotaphopeltis hotamboeia, *Homoroselaps lacteus*, *Lycodonomorphus inornatus*, *Psammophis crucifer*, *P. leightoni*, *Psammophylax rhombeatus*, and *Rhinotyphlops lalandei*.

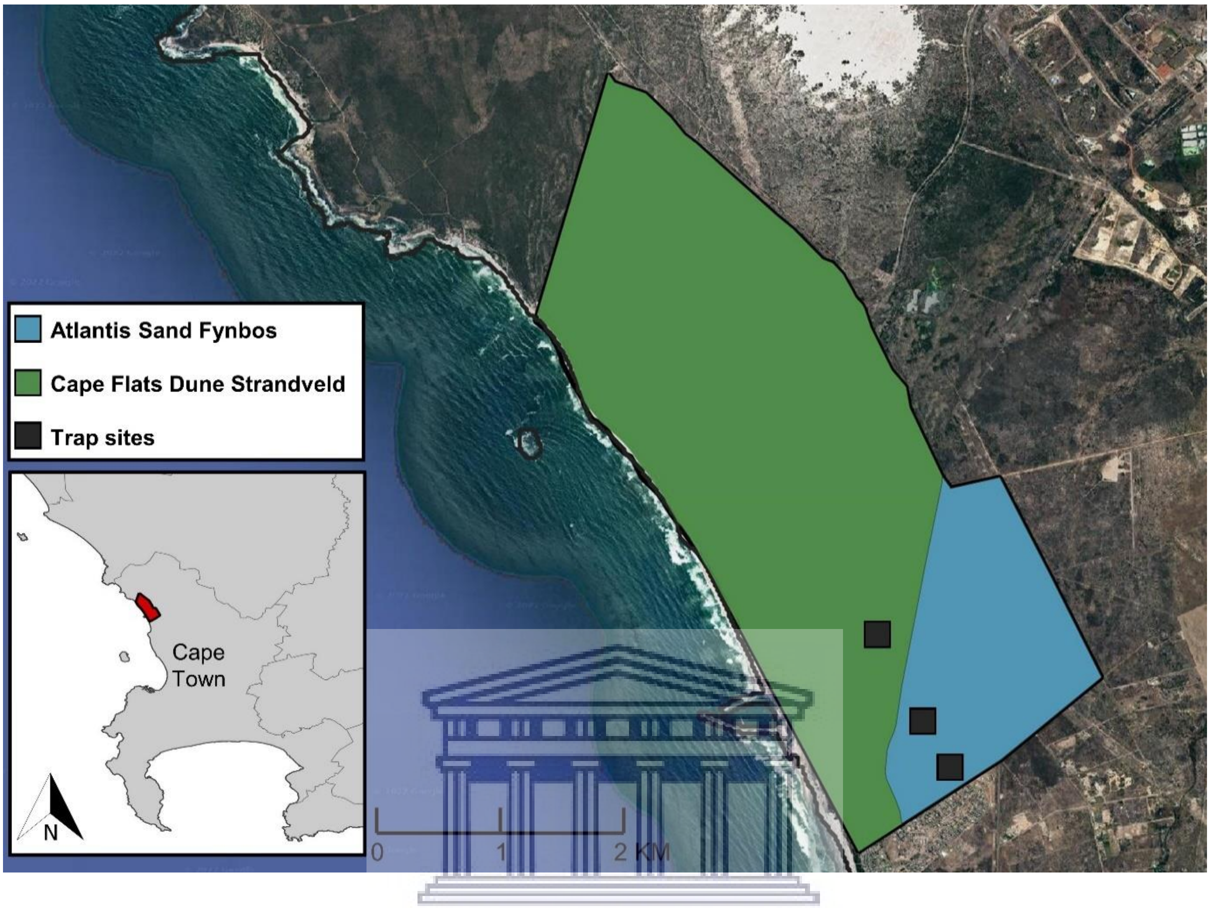

Fig. 6.1: Map of Koeberg Private Nature Reserve (KNR) with vegetation types overlaid above the reserve. Black squares represent approximate locations of trap arrays.

6.3.3 Sampling protocol

I set up three trap arrays in Koeberg Private Nature Reserve in July 2020 to catch egg-eaters at known locations. Each array consisted of 100 shutterply artificial cover objects (ACOs) individually measuring 600 x 600 x 18 mm, spaced ~15 metres apart in a grid of 10 x 10 (Fig. 6.2). One array was positioned in Strandveld vegetation and the other two in Fynbos vegetation. The two Fynbos sites were similar in topography and vegetation but differed in perceived openness of vegetation cover, with the southernmost site considered to be denser. Sampling took place intermittently between August 2020 and April 2022. Sampling effort included 15 sampling occasions in which all 300 ACOs were checked, totalling 4500 possible detection events. Snakes captured underneath ACOs were weighed to the nearest 0.1 g using a digital scale and measured to the nearest 0.01 mm using a tape measure. Measurements included snout-vent length (SVL) and tail length. Each captured snaked was uniquely marked by clipping a sequence of ventral scales (Plummer & Ferner 2012) before being released.

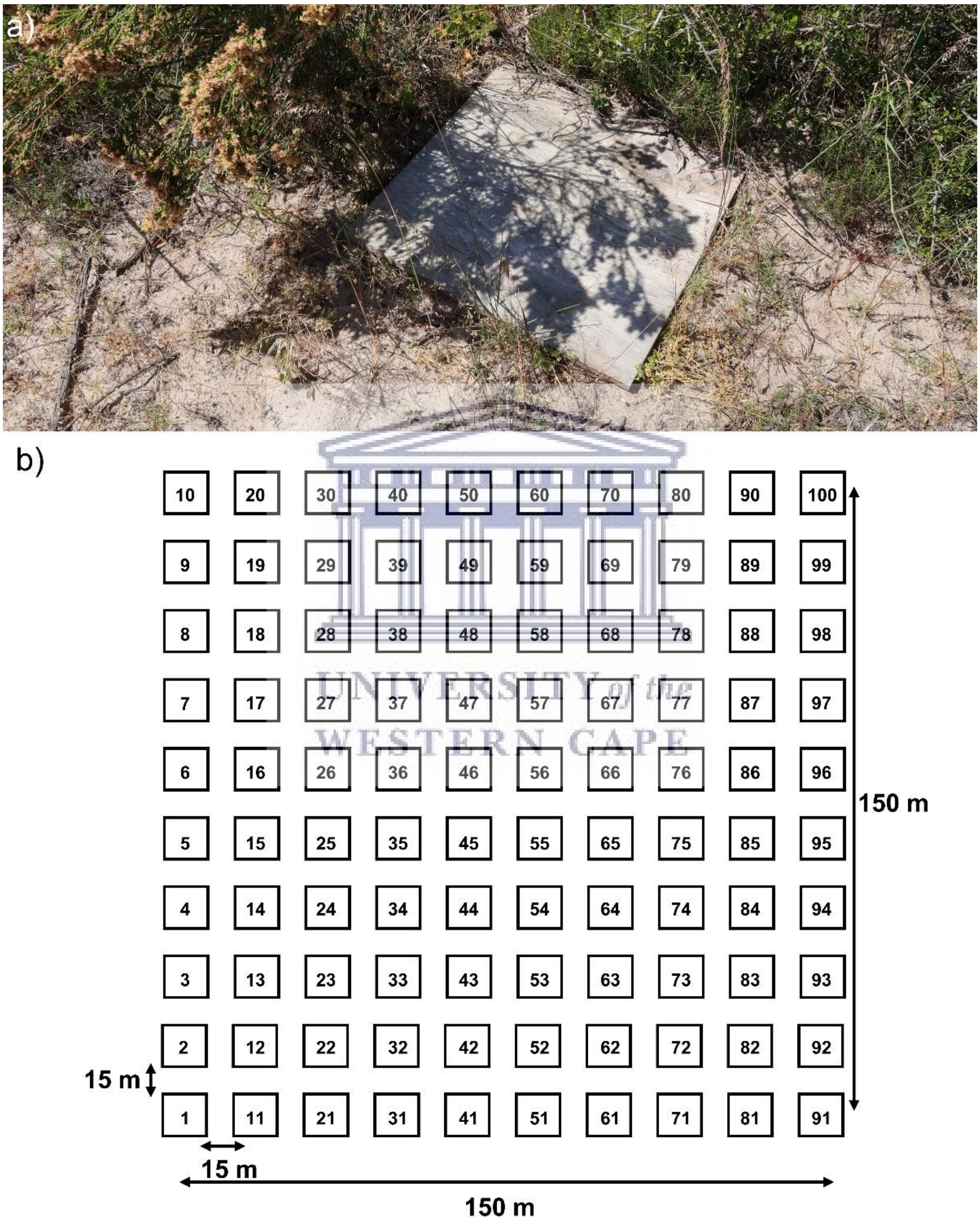

Fig. 6.2: a) An example of an artificial cover object used to capture snakes at Koeberg Private Nature Reserve, and b) schematic diagram of the trap placement design.

6.3.4 Estimating population density

I estimated the population densities of *Dasypeltis scabra* at Koeberg Private Nature Reserve by fitting SECR models to snake capture data and GPS location data of ACOs at each site using the ‘SECR’ package (Efford 2018) in R software v 4.1 (R Core Team 2021). Because ACOs could potentially detect multiple individuals on any sampling event, I ran models using the ‘multi’ detector under a half-normal detection function (Efford 2018). I applied a 100-metre buffer masked around all ACOs for each site. Initial models were standardized with constant detection parameters (i.e. $[(D) \sim 1, g0 \sim 1, \sigma \sim 1]$). To increase the accuracy of models I included snake SVL as an additional, individual-dependent continuous covariate (ranging from 218 – 583 mm) for subsequent models. For each site, I ran three additional models in which SVL was added as a covariate on $g0$, on σ, and both $g0$ and σ respectively. Model performance was compared using Akaike Information Criterion standardized for small sample sizes (AICc; Akaike 1973) scores.

6.4 Results

6.4.1 Snake captures

Dasypeltis scabra was captured only 13 times across 11 individuals collectively between all sites. Six individuals were captured at the Strandveld site (total detections = seven, recaptures = one), and five individuals were captured at the southernmost Fynbos site (total detections = six, recaptures = one). However, no snakes were captured at the northernmost Fynbos site apart from one occasion in which the shed skin identified as belonging to *D. scabra* was found underneath an ACO. This site was therefore excluded from further analyses. Detections between the two sites at which snakes were caught were similar (Chi-square test: $X^2_{\mathrm{df}=1} = 0.077$, $P = 0.782$). In addition, size distributions of captured snakes of these sites did not differ for both SVL (Kolmogorov-Smirnov test: $D = 0.457$, $P = 0.434$) and mass variables

(Kolmogorov-Smirnov test: $D = 0.657$, $P = 0.116$), indicating similarities in population structure between sites.

6.4.2 Population density

At the Strandveld site, the best performing model (in terms of lowest AICc score) was the [D(site), $g0$(.), σ(SVL)] model (Table 6.1). Contrastingly, the best performing model at the southern Fynbos site was the [D(site), $g0$(SVL), σ(.)] model. However, at both sites, the [D(site), $g0$(.), σ(SVL)] and [D(site), $g0$(SVL), σ(.)] models each produced similarly low dAICc values considerably less than two. Comparatively the basic models and the most parameterized models did not produce dAICc scores less than two at either site. Population density estimates of *Dasypeltis scabra* were similar throughout all models for each respective site (Table 6.2). Density estimates ranged from 7.266 – 8.575 snakes ha^{-1} at the Strandveld site and 5.262 – 6.007 snakes ha^{-1} at the Fynbos site. However, owing to the low capture rates of snakes the confidence intervals on these density estimates were high, ranging from as low as one to as high as 56 snakes ha^{-1}.

Table 6.1: Model performance of four SECR models across two sites with associated AIC scores. Models with lower AICc values indicate best performing models. Model parameters include population density (*D*), capture probability (*g*0), and spatial scale (σ). Covariates include snout-vent lengths of captured snakes (SVL). The best performing model for each site is highlighted in boldface.

Site	**Model**	**No. parameters**	**Log likelihood**	**AIC**	**AICc**	**dAICc**	**AICcwt**
Strandveld site	[*D*(site), *g*0(.), σ(.)]	3	-46.908	99.816	111.816	3.685	0.074
	[*D*(site), *g*0(SVL), σ(.)]	4	-45.068	96.135	108.135	0.004	0.463
	[*D*(site), *g*0(.), σ(SVL)]	**4**	**-45.066**	**96.131**	**108.131**	**0.000**	**0.464**
	[*D*(site), *g*0(SVL), σ(SVL)]	5	-42.060	92.120	132.120	23.989	0.000
Southern Fynbos site	[*D*(site), *g*0(.), σ(.)]	3	-41.391	88.783	112.783	3.519	0.079
	[*D*(site), *g*0(SVL), σ(.)]	**4**	**-39.632**	**85.264**	**109.264**	**0.000**	**0.461**
	[*D*(site), *g*0(.), σ(SVL)]	4	-39.632	85.265	109.265	0.001	0.460
	[*D*(site), *g*0(SVL), σ(SVL)]	5	-39.634	87.267	111.246	3.486	0.069

Table 6.2: Density estimates of *Dasypeltis scabra* from four SECR models at two sites. *D* = estimated number of individuals per hectare, *g0* = capture probability, *σ* = spatial scale parameter. The best performing model for each site is highlighted in boldface.

Site	**Model**	***D* (95% CI)**	***g*0 (95% CI)**	***σ* (95% CI)**
Strandveld site	*D*(site), *g*0(.), *σ*(.)	7.266 (1.021 – 51.694)	0.002 (0.000 – 0.031)	24.083 (6.368 – 91.079)
	D(site), *g*0(SVL), *σ*(.)	8.295 (0.647 – 106.354)	0.002 (0.000 – 0.091)	25.194 (5.847 – 108.546)
	***D*(site), *g*0(.), *σ*(SVL)**	**8.282 (1.210 – 56.659)**	**0.002 (0.000 – 0.038)**	**22.740 (6.832 – 75.691)**
	D(site), *g*0(SVL), *σ*(SVL)	8.575 (2.930 – 25.093)	0.002 (0.000 – 0.018)	23.717 (6.898 – 81.537)
Southern Fynbos site	*D*(site), *g*0(.), *σ*(.)	5.262 (0.791 – 35.017)	0.003 (0.000 – 0.049)	19.728 (6.003 – 64.840)
	***D*(site), *g*0(SVL), *σ*(.)**	**5.794 (0.926 – 36.246)**	**0.002 (0.000 – 0.677)**	**21.470 (5.626 – 81.933)**
	D(site), *g*0(.), *σ*(SVL)	5.594 (0.812 – 42.762)	0.003 (0.000 – 0.092)	17.765 (5.092 – 43.585)
	D(site), *g*0(SVL), *σ*(SVL)	6.007 (1.175 – 30.708)	0.003 (0.000 – 0.017)	18.418 (5.207 – 51.229)

6.5 Discussion

My results demonstrate that *Dasypeltis scabra* occurs at high densities at Koeberg Private Nature Reserve. While snake captures and recaptures were low at each site (including one site that produced no captures), estimates of population density ranged from 5.79 snakes ha^{-1} in open, Fynbos vegetation to 8.28 snakes ha^{-1} in dense, Strandveld vegetation. However, owing to limited snake detections, a problem that is often unavoidable for species with low detectability (Maritz & Alexander 2012; Kolanek & Bury 2021), model estimates had wide confidence limits. The estimates I obtained should thus be interpreted with the above in mind. Nevertheless, my results are of interest as they provide one of the few estimates of population density for any species of African snake.

Population estimates of African snakes are rare, making it difficult to compare my results to other African species. However, the few studies available suggest that African snake densities can vary widely between species. Jacobsen (1982) estimated the density of *Thelotornis capensis* as 1.32 snakes ha^{-1} in the Nylsvley Nature Reserve in Limpopo, South Africa. Maritz & Alexander (2012) estimated the population density of *Bitis schneideri*, a small-bodied (< 260 mm SVL) viperid that occurs along the west coast of Namaqualand as 7.52 – 8.31 snakes ha^{-1}. More recently, Tokota (2021) predicted population densities of sympatric *Psammophis crucifer* and *Psammophylax rhombeatus* across several sites in Koeberg Private Nature Reserve as 1.02 – 14.03 snakes ha^{-1}. My estimates of *Dasypeltis scabra* density (5.79 – 8.28 snakes ha^{-1}) are similar to those of *B. schneideri* and fall within the range of *P. crucifer* and *P. rhombeatus* respectively.

Interestingly, my estimates of snake density produced here, as well as those of Maritz & Alexander (2012), and Tokota (2021) are considerably higher (by more than an order of magnitude) compared to estimates of large-bodied snakes from West Africa. In southern

Nigeria, Luiselli (2006b) produced estimates of 0.16 and 0.10 snakes ha^{-1} for *Bitis gabonica* and *B. nasicornis* respectively. Similarly, Luiselli et al. (2001) estimated a density of 0.11 snakes ha^{-1} for *Dendroaspis jamesonii* in the same region. It is not clear whether these pronounced differences in snake densities between southern and West African species are due to differences in species ecology (for example body size, biome use, prey abundance etc.), geographic location, choice of statistical models, or other factors. However, large species generally tend to have lower population densities than smaller species (Marquet et al. 1995) and differences in snake body size are likely the most responsible cause of these trends. More data from a larger sample of African species are required to robustly discern these patterns.

While a limited number of studies exist for African snake population ecology, several studies on species from other regions are available. In North America, estimates of colubrid snake density range from as few as < 1 snake ha^{-1} (*Pantherophis obsoletus* in Kansas, Fitch 1982) up to > 1200 snakes ha^{-1} (*Liodytes alleni* and *Liodytes pygaea* in Florida, Godley 1980). In Europe, grass snakes (*Natrix natrix*), one of the more abundant snake species in the region, occur at densities of 4.8 – 52.4 snakes ha^{-1} in eastern England (Sewell et al. 2015), 3.6 snakes ha^{-1} in central Germany (Mertens 1995), and 4.5 – 13 snakes ha^{-1} in central Italy (Rugiero et al. 2002). Tiger snakes (*Notechis scutatus*) occur at densities of 4 – 25 snakes ha^{-1} on offshore islands around Australia (Bonnet et al. 2002). Invasive brown tree snakes (*Boiga irregularis*), a close relative of *Dasypeltis* (Zheng & Wiens 2016), occur at densities of 8 – 50 snakes ha^{-1} on various parts of the islands of Guam (Rodda et al. 1992; Smith et al. 2016). My estimates for *Dasypeltis scabra* are in the range of many of these snakes but do not match the higher densities observed for others.

Dasypeltis scabra is one of the primary threats to the nesting success of birds across sub-Saharan Africa (Bates & Little 2013; Barends & Maritz 2022a). While the exact number of bird eggs consumed by these snakes each year is unknown, laboratory-based experiments suggest that under certain conditions individuals require ~3 eggs to maintain annual body condition (Chapter 5). My estimates of *D. scabra* density at Koeberg Private Nature Reserve were 5.79, 8.28, and 0 snakes ha^{-1} at three respective sites (mean = 4.69 snakes ha^{-1}). At an average of 4.69 snakes ha^{-1} across the reserve, by process of extrapolation, this suggests a total of at least 13 600 snakes in the reserve. Should each snake consume the minimum required three eggs per year (Chapter 5) then > 40 000 eggs could potentially be consumed by *D. scabra* in the reserve annually. At 5.79 snakes ha^{-1} this translates to > 50 000 eggs, and at 8.28 snakes ha^{-1} it becomes > 72 000 eggs. While *D. scabra* are not the only nest predators at Koeberg, they are the primary consumers of eggs (Nalwanga et al. 2004) and feasibly could consume eggs at such high numbers. Although no studies have investigated annual consumption by wild snakes in Africa, one study from North America (Willson & Winne 2016) found that aquatic snakes in a 5.4 ha South Carolina wetland occur at a density of 171 snakes ha^{-1} and collectively consume over 55 000 individual amphibians annually. In comparison, the *D. scabra* population at Koeberg Private Nature Reserve occurs at a much lower density but occupies a much larger geographic area and so could feasibly consume similarly high numbers of prey.

The high densities and predicted egg consumption of *Dasypeltis scabra* I observed may in part be facilitated by the diversity and breeding ecology of the bird community at Koeberg Private Nature Reserve. At least 230 species of birds occur at Koeberg Private Nature Reserve (Brooks & Ryan 2020). Comparatively, only five species of amphibians, 25 species of reptiles, and < 50 species of mammals are present (Harrison 2008; Forgus 2018). Egg sizes of the Koeberg bird community range from 9.8 (Cape penduline-tit, *Anthoscopus minutus*) to 121 mm (common ostrich, *Struthio camelus*) in diameter (Chapter 4). Moreover, birds at Koeberg typically nest in low shrubs or on the ground (Nalwanga et al. 2004; Rohwer et al. 2017), where they are easily accessible for predation by *D. scabra*. Eggs are therefore accessible to snakes of all size classes. In addition, many common species in the reserve such as Karoo prinias (*Prinia maculosa*), Karoo scrub-robins (*Erythropygia coryphaeus*), and Cape robin chats (*Cossypha caffra*) often re-lay clutches (sometimes multiple times) following nest failure (Tarboton 2011), thereby adding to the number of eggs annually available. Thus, it is likely that the high abundance and easy access to varying sizes of bird eggs sustain the large population of *D. scabra* at Koeberg Private Nature Reserve and likely other areas.

My study provides one of the few estimates of African snake population density and size. However, these estimates were based on models built on a limited number of snake detections. As a result, model performance suffered from the low sample size and so the estimates I obtained had wide confidence intervals. For many cryptic species like snakes, the problem of low detectability is often unavoidable and so this issue is prevalent among similar studies (Maritz 2012; Tokota 2021). However, this does require that these limitations in model accuracy be taken into consideration when interpreting my results. To produce more robust models, a higher sampling frequency is likely required to ensure greater capture rates with more recaptures. Future attempts at snake population estimates, particularly when using an SECR approach, should consider the sampling effort required to produce accurate estimations.

Understanding predator population size is vital towards quantifying their ecological importance. Unfortunately, many predators, including most species of snakes, are difficult to study and their population ecology remains unknown. My study contributes to the limited body of knowledge concerning the population density of African snakes. I demonstrate that *Dasypeltis scabra* occurs at a relatively high density similar to those of other southern African snakes and thus has the potential to remove a large number of bird eggs from several biological communities each year. It is therefore likely that these, and other species of snakes, are important ecosystem components across a variety of ecosystems throughout Africa, thus debunking the perception that infrequently encountered species are rare and ecologically unimportant. Further investigations, particularly robust field studies, are required to ascertain these claims, but my results provide a promising outlook towards highlighting the functional importance of snakes.

6.6 Acknowledgements

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Chapter 7: Specialized Morphology, Not Relatively Large Head Size, Facilitates Competition Between a Small-Bodied Specialist and Large-Bodied Generalist Competitors

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7.1 Abstract

Interspecific competition for limited resources should theoretically occur between species that are morphologically similar to each other. Consequently, species that reduce competition by adapting to specialize on a specific resource should be morphologically disparate to sympatric contemporaries and show evidence of phenotypic specialization. However, few studies have compared the morphologies of specialist and generalist competitors. Here, I measured and compared body and head dimensions of preserved museum specimens of each of four, syntopic snake species from southern Africa: the obligate bird egg-eating rhombic egg-eater (*Dasypeltis scabra*), and the facultative bird egg-eating boomslang (*Dispholidus typus*), cape cobra (*Naja nivea*), and mole snake (*Pseudaspis cana*). Given the physical challenges of consuming bird eggs in snakes, I predicted that consumption of bird eggs would be facilitated by the evolution of relatively larger heads in the smaller-bodied *Dasypeltis*. I found that head size was not phylogenetically conserved in the clades of these taxa and that contrary to my expectations, the specialist egg-eaters evolved to possess significantly smaller heads relative to body size than their competitors. I found a positive relationship between dietary niche breadth and head size within these species and their close relatives. Thus, relatively large-headed species have evolved diverse diets that overlap with the restricted diets of the small-headed specialist thereby producing this atypical competitive interaction. My findings suggest that specialized adaptations can decouple typical body-size constrained competition dynamics between sympatric snake species and highlight the complexity of the origins of dietary specialization.

7.2 Introduction

Sympatric species that are ecologically and morphologically similar to each other are predicted to compete for shared resources (Toft 1985; Arthur 1987; Ye et al. 2019). This competition can result in selection for differences in ecology and morphology that act to reduce competition between such species. As a consequence, species that specialize on a narrow range of the available resources to reduce interspecific competition by efficiently exploiting a specific niche often have unique adaptive morphology that differentiates them from sympatric competitors (Schoener 1974; Pianka 1978; Mori & Vincent 2008). Accordingly, studying the links between phenotypic specialization and niche utilization across interspecific competitors has the potential to elucidate the selective pressures behind factors like resource partitioning that have ultimately driven biological diversification (Roughgarden 1983; McGill et al. 2006). However, comparative studies that seek to quantify phenotypic specialization of ecological specialists relative to generalists are surprisingly sparse (Mori & Vincent 2008).

Generally, competition between species over shared resources can be predicted based on phenotypic similarities (Pianka 1978; Schoener 1983; McGill et al. 2006). For example, morphologically and taxonomically similar species of comparable body size are likely to compete with each other over specific resources because these species are likely to share similar ecological constraints (Schoener 1974; Bloch et al. 2011). As such, body size can act as an effective predictor for interspecific competition between similar organisms within biological communities comprised of a range of variably-sized species (Case et al. 1983; Alatalo & Moreno 1987; LaBarbera 1989; Robertson 1998; Luiselli 2006a). Additionally, body size can also act as a predictor of competitive superiority between competing species (Schoener 1983; Persson 1985; Morin & Johnson 1988; Nakayama & Fuiman 2010). Typically, larger-bodied species are competitively superior to smaller-bodied species in interference competition but smaller-bodied species are more efficient at exploitation competition (Alatalo & Moreno 1987; Nascimento et al. 2011). As a result, body size is often strongly linked to dynamics of competition and resource partitioning (Luiselli 2006a) and potentially plays an important role in the phenotypic specialization of competing species.

Snakes represent an ideal group of terrestrial vertebrate predators in which to empirically test hypotheses relating to adaptive morphological differences between dietary specialists and generalists. Snakes are restricted in terms of the prey that they can consume as they are unable to mechanically reduce the sizes and process their captured prey (Greene 1997; Mori & Vincent 2008), thereby making them gape-limited predators. As such, snake gape size, and therefore head size, can be directly linked to the range of prey that snakes consume (Arnold 1993; Cundall & Greene 2000; Cundall 2019), thus allowing for the inference of direct relationships between changes in the functional morphology of snake feeding apparatus and the consumption of specific prey (Rodríguez-Robles et al. 1999; Vincent et al. 2006; Moon et al. 2019). For example, North American natricine snakes that feed exclusively on fish have longer quadrate bones and increased swallowing performance of large fish prey to congeneric generalists (Vincent et al. 2009).

Snakes that consume large prey are typically able to do so because they possess specialized adaptive morphology, or, are simply large-bodied and have large heads (Cundall & Greene 2000; Moon et al. 2019). Generally, snake species with larger heads can consume a broader range of prey than those with smaller heads (Arnold 1993; Greene 1997; Cundall & Greene 2000). As a result, large-bodied snakes are predicted to have a wide dietary niche (Shine 1991b; Arnold 1993; Luiselli 2006a; Moon et al. 2019) and generalist diets. Conversely, dietary specialists that only consume a limited number of prey types should showcase predictable phenotypical adaptations in their head elements that facilitate the ingestion of their preferred prey (Mori & Vincent 2008).

As a source of food for snakes, bird eggs are generally infrequently utilized (Barends & Maritz 2022a) owing largely to the mechanical difficulties associated with bird egg consumption (de Queiroz & Rodríguez-Robles 2006; Gartner & Greene 2008). Bird eggs are often bulky, hard, round, and slippery (Tarboton 2011; Bates & Little 2013), making them difficult for snakes to ingest using traditional prey transport mechanisms (Cundall & Greene 2000; Jayne et al. 2018). Consequently, the majority of snake species that consume bird eggs are large-bodied generalist feeders with large gapes that allow them to circumvent the challenges of ingesting bird eggs (Barends & Maritz 2022a). As such, species that specialize on bird eggs should theoretically possess head and jaw elements that provide a gape size equal to or larger than generalist competitors of the same body size allowing them to better ingest and more efficiently exploit this mechanically challenging prey type. Although hypotheses relating to egg-eating performance have been tested between unrelated, allopatric species from different continents (Gartner & Greene 2008) they remain untested amongst specialist and generalist bird egg competitors within real-world snake communities.

African egg-eater snakes of the genus *Dasypeltis* represent a model group of species for comparative investigations relating to phenotypic specialization for feeding as all members of the genus are bird egg specialists (Branch 1998; Alexander & Marias 2007; Bates & Little 2013). Occurring throughout sub-Saharan Africa and parts of the Arabian Peninsula, all members of *Dasypeltis* obligately feed only on bird eggs (Bates & Little 2013; Bates & Broadley 2018) and possess a host of unique morphological adaptations that functionally accommodate the exploitation of this prey type (Gans 1952; Gans 1974; Gartner & Greene 2008). Morphological adaptations in *Dasypeltis* include highly stretchable neck, jaw, and mouth tissue, a buccal cavity devoid of teeth, as well as modified vertebral hypapophyses that allow them to ingest and crush bird eggs before regurgitating the shell remains (Gans 1952; Broadley 1990; Branch 1998; Alexander & Marais 2007).

Somewhat surprisingly, members of *Dasypeltis* are not particularly large-bodied snakes (~160 – 1000 mm SVL; Bates & Broadley 2018). These snakes are demonstrably smaller in absolute body size relative to competing snakes that also consume bird eggs. Southern African snakes that are known consumers of bird eggs and occur sympatrically with *Dasypeltis* such as Cape cobras (*Naja nivea*; Layloo et al. 2017), boomslang (*Dispholidus typus*; Smith et al. 2019), and mole snakes (*Pseudaspis cana*; Underhill et al. 2009) each out-size rhombic egg-eaters in their respective absolute body size, with adults of each species reaching up to 2 m in total length (Alexander & Marais 2007). Given the obvious differences in absolute body size between *Dasypeltis* and their competitors, adult *Dasypeltis* are unlikely, in absolute terms, to have longer or wider heads than adults of generalist, facultative egg-eating competitors. However, *Dasypeltis* may have evolved larger heads (relative to their body size) to produce heads that allow them to compete with larger-bodied competitors that possess absolutely larger heads.

I examined head size variation and its evolution among four, sympatric, bird-egg-eating snakes including the egg-eating specialist, *Dasypeltis scabra*, and three egg-eating generalists: *Naja nivea*, *Dispholidus typus*, and *Pseudaspis cana*. I hypothesised that *D. scabra* has experienced selection for larger head size, resulting in head sizes that are comparable to those of its larger-bodied, generalist competitors. I test this hypothesis by 1) quantifying and reconstructing head size across a phylogeny including the four target species, plus 30 other closely related species and 2) explicitly comparing head dimensions of the four target species. To provide context to my comparisons, I additionally examine the relationship between the dietary niche breadth and head sizes of snakes to better understand the evolutionary dynamics that characterise the interplay of dietary specialization, trophic morphology, and interspecific competition of these species and selected closely related snake taxa.

7.3 Methods

7.3.1 Phylogenetic coverage

Because the four study species (*Dasypeltis scabra*, *Dispholidus typus*, *Naja nivea*, and *Pseudaspis cana*) are highly divergent in their phylogenetic relatedness (Tonini et al. 2016; Zheng & Wiens 2016), differences in their morphologies and diet may reflect phylogenetic trends in the evolutionary histories of their respective clades rather than adaptive responses to ecological correlates like competition for food. I thus sought to take common ancestry into account in my comparisons of these aspects. I increased the taxonomic coverage by collecting morphological and dietary data for the four target species and 30 additional snake taxa closely related to them, resulting in an expanded 34-taxon dataset (Table S7.1). These additional species comprised several closely related members of the Colubridae, Elapidae, and Lamprophiidae *sensu lato* (including Pseudaspididae) families, respectively. I pruned the time-calibrated phylogeny of squamate reptiles presented in Zheng & Wiens (2016) to only include the selected taxa for use in phylogenetic analyses (Fig. S7.1).

7.3.2 Morphological measurements

I measured the bodies and heads of preserved specimens of the study species (*Dasypeltis scabra*: *n* = 19, *Dispholidus typus*: *n* = 15, *Naja nivea*: *n* = 17, and *Pseudaspis cana*: *n* = 14) and the additional taxa comprising the expanded dataset housed in herpetology collections at Iziko South African Museum in Cape Town, Bayworld Museum in Port Elizabeth, and the University of the Western Cape (Table S7.1). I only included measurements from adult specimens and used equal numbers of male and female specimens as best as I could to minimize the effects of ontogenetic shifts and sexual size dimorphism on measurements. For each individual, I measured the following: snout-vent length (SVL), tail length, head height, head length (the distance between the posterior of the parietal scale to the snout), head width, and lower jaw length (the distance between the dentary and the retroarticular process). See Vincent et al. (2006) for justification of the selection of these specific morphological measures concerning snake feeding apparatus. I measured SVL and tail length to the nearest 1 mm using a measuring tape and measured all head dimensions using digital calipers (accuracy: 0.001 mm). Summarized morphology measures are presented in Table S7.2.

7.3.3 Dietary niche

To compare the relative importance of bird eggs within the diets of the four study species and their relatives I collated dietary information for each species from the literature and citizen science reports of feeding records published online. I estimated the consumption of different prey as a proportion for each snake species using the following prey categories: amphibians, birds, bird eggs, lizards, mammals, snakes, and other prey. Using estimated proportions of prey use, I then calculated Levins' measure of niche breadth (Levins 1968) based on the equation $B = 1/\Sigma p_i^2$ where B is Levins' niche breadth and p_i is the proportion of individuals consuming a particular prey type. I then standardised this measure to range between zero and one using the equation $B_A = (B - 1) / (n - 1)$, where B_A is Levin's standardised niche breadth, and n is the total number of prey classes.

7.3.4 Statistical analyses

I performed all statistical analyses using IBM SPSS v23.3 (IBM Corp 2021) and R software v4.1 (R Core Team 2021). To meet the assumptions of homoscedasticity and ensure that all data were normally distributed I log-transformed all morphological body and head size measures. To examine covariation within head measures and relevant PC axes independently of body sizes across study species, I created a variance-covariance matrix of all head measures relative to body size for each species. I calculated this matrix by regressing all log-transformed head measures against log-transformed SVLs to generate size-adjusted residual contrast values for each specimen. I then input these size-adjusted contrasts into a principal component analysis (PCA) using the prcomp function of the 'Stats' R package (R Core Team 2021) to calculate the variance-covariance matrix. I used a scree plot and the broken stick method (Jackson 1993) to identify significant principal component axes. The broken stick method compares the variances of each component and identifies those that explain more variance than expected as significantly important. I then averaged the values across all specimens of each species for each significant component.

To remove the effects of phylogeny on the above analysis, I also calculated a second matrix that took common ancestry into account using the expanded dataset. To create this phylogenetically corrected covariance matrix, I performed a phylogenetic PCA (pPCA) using the phyl.pca function of the 'Phytools' R package (Revell 2012). For this analysis, I used size-adjusted contrast values for the expanded 34-taxon dataset in conjunction with the phylogeny. I then identified significant PC axes and estimated relative head size for each species in a similar manner to the non-phylogenetically corrected PCA analysis.

To ensure that differences in head size between the four study species were not significantly driven by patterns of phylogenetic conservatism of head morphology among those species and their relatives, I tested for evidence of a phylogenetic signal in general head size (i.e. average scores derived from the main principal component, hereafter PC 1) across the expanded 34-taxon phylogeny. I tested for phylogenetic signal by calculating Blomberg's *K* (Blomberg et al. 2003). Blomberg's *K* values lower than one indicate that traits of closely related species resemble each other less than expected under a Brownian motion model of evolution whereas *K* values greater than one suggests stronger trait similarity between close relatives (Blomberg et al. 2003).

I identified the most appropriate model of evolution for general head size across the phylogeny by comparing four evolutionary models, namely the Brownian motion, Early-burst, Ornstein-Uhlenbeck, and white noise models of evolution using the ‘Geiger’ R package (Pennell et al. 2014). I selected the most appropriate model based on each model’s Akaike Information Criterion corrected for small sample size (AICc; Akaike 1973) scores. I then visually demonstrated evolutionary divergences in head morphology between study species and their relatives by performing a Maximum Likelihood ancestral reconstruction analysis of head size across the phylogeny. I used the anc.ML function of the ‘Phytools’ R package, to reconstruct averaged PC 1 scores of each species across the phylogeny under the best performing model of evolution (see Results). I visualized these projections across the phylogeny using the contMap function of the same package.

To test the hypothesis that head size relative to body size differed between *Dasypeltis scabra*, *Dispholidus typus*, *Naja nivea*, and *Pseudaspis cana*, I used a multivariate analysis of variance (MANOVA) to compare covariation in head sizes across these four species. For this analysis, I included the body size-adjusted measures of head height, head length, head width, and lower jaw length, as well as the significant PC axes from the PCA analyses (i.e. PC 1, see Results below) and the dietary niche breadth of each species (Levins B_A) as the dependent variables, and I used sex and species as the grouping factors. I also included the associated Bonferroni *post hoc* pairwise comparisons for further examinations of differences of each variable between each combination of species (see Shine et al. 2006).

Lastly, I examined the relationship between relative head size and dietary specialization within the four study species. I did this by performing ordinary least squares regression analyses comparing average PC 1 estimates and Levins’ B_A values of each species. I also performed a similar ordinary least squares regression analysis using the PC 1 values derived from the pPCA of the extended 34-taxon dataset to take phylogeny into account. I ran regressions involving pPCA scores twice, once using only the four target species, and once with the 34-taxon dataset.

7.4 Results

7.4.1 Summarized head size measures

The non-phylogenetically corrected, size-adjusted PCA performed across head measures yielded only a single significant axis (PC 1; Fig. S7.2). This axis explained 83% of the total variation in head size data, with all head measures having loaded positively (> 0.50; Table S7.3). The phylogenetically corrected, size-adjusted pPCA yielded similar results. Again, only PC 1 was significant (Fig. S7.3) and explained 87% of the total variation in head size data. Each of the head measures loaded positively on PC 1 and had similar magnitudes of co-variation between them when correcting for common ancestry (> 0.89, Table S7.4).

7.4.2 Relative head size conservatism and ancestral reconstruction

The Brownian motion model of evolution provided the best fit for my analyses of head size evolution across the phylogeny based on model AICc scores (Table S7.5). Phylogenetic signal analysis revealed a significant phylogenetic signal was present for head size relative to body size across the tree ($K = 0.887$, $P = 0.001$). This result indicates that the sizes of the heads of closely related species resembled each other less than expected under a Brownian motion model of evolution but were more similar to each other than to species drawn from the tree at random. My reconstruction of relative head sizes (i.e. PC 1) across the phylogeny shows that while several species share similar head morphology to their close relatives, several transitions from small head size to large head size occurred across some lineages (Fig, 7.1). These transitions were present in all lineages containing bird egg-eating species in the dataset (i.e. *Dispholidus typus,* all members of *Naja, Pseudaspis cana,* and *Toxicodryas blandingii*) but did not occur between *Dasypeltis* and their ancestors.

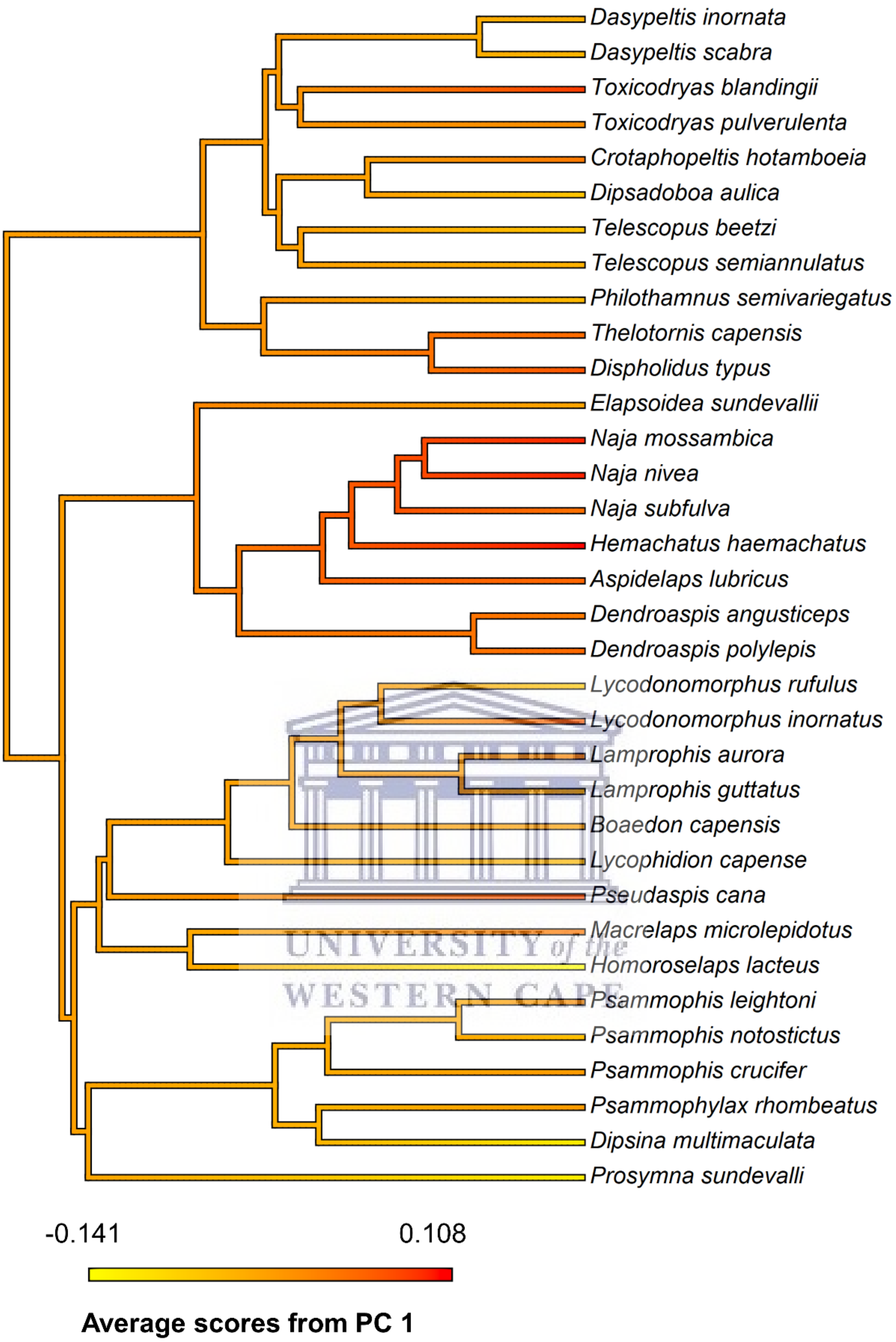

Fig. 7.1: Ancestral reconstruction of head size covariation relative to body size (PC 1) derived from principal component analyses on size-adjusted head measures for 34 snake taxa.

7.4.3 Comparisons of head size

Body size-adjusted head morphology measures were distinctly separated across *Dasypeltis* and its competitors (Fig. 7.2). The results of my body size-adjusted MANOVA tests (Homogeneity of slopes test: diet – size: $F_{3, 61} = 0.122$, $P = 0.947$; sex – size: $F_{1, 63} = 0.231$, $P = 0.632$) confirmed that there were significant differences in average head measures between these species ($F_{12, 154} = 17.352$, *Wilk's Lambda* = 0.104, $P < 0.001$) but not between sexes ($F_{5, 53} = 0.463$, *Wilk's Lambda* = 0.958, $P = 0.802$) or between the interaction of species and sex ($F_{15, 146} = 0.235$, *Wilk's Lambda* = 0.937, $P = 0.986$). The non-significance of sex on the effects of morphological measures suggests that differences in head sizes are not present as a result of sexual size dimorphism.

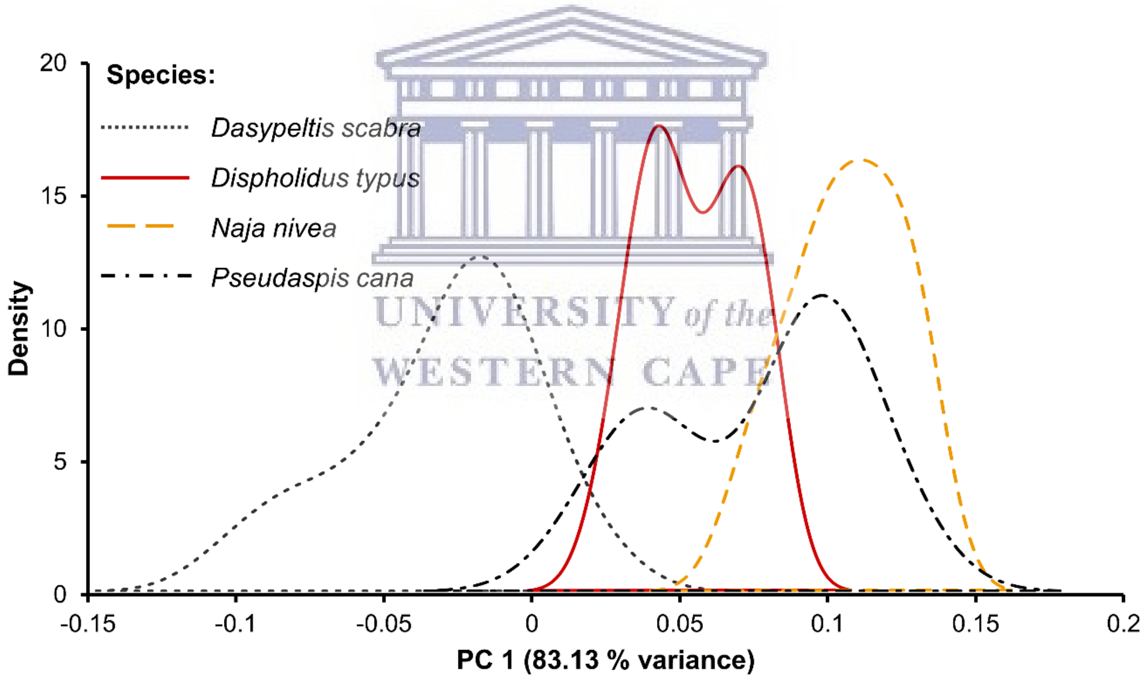

Fig. 7.2: Kernel density estimation of the first PC axis (PC 1) of PCA performed on size-adjusted head measures of four snake species.

Overall, *Dasypeltis* had significantly smaller head dimensions relative to body size than boomslang, cape cobras, and mole snakes for all head measures (Fig. 7.3) as well as for the summarized relative head size derived from PC 1. *Dasypeltis* had smaller head measures in absolute terms as well (Table S7.2). Comparisons between the facultative bird egg-eating snakes showed that cape cobras differed in head shape to boomslang and mole snakes respectively for several head measures whereas the head measures of boomslang and mole snakes were relatively similar in most cases (Table 7.1). All four species significantly differed from each other in their dietary niche breadths.

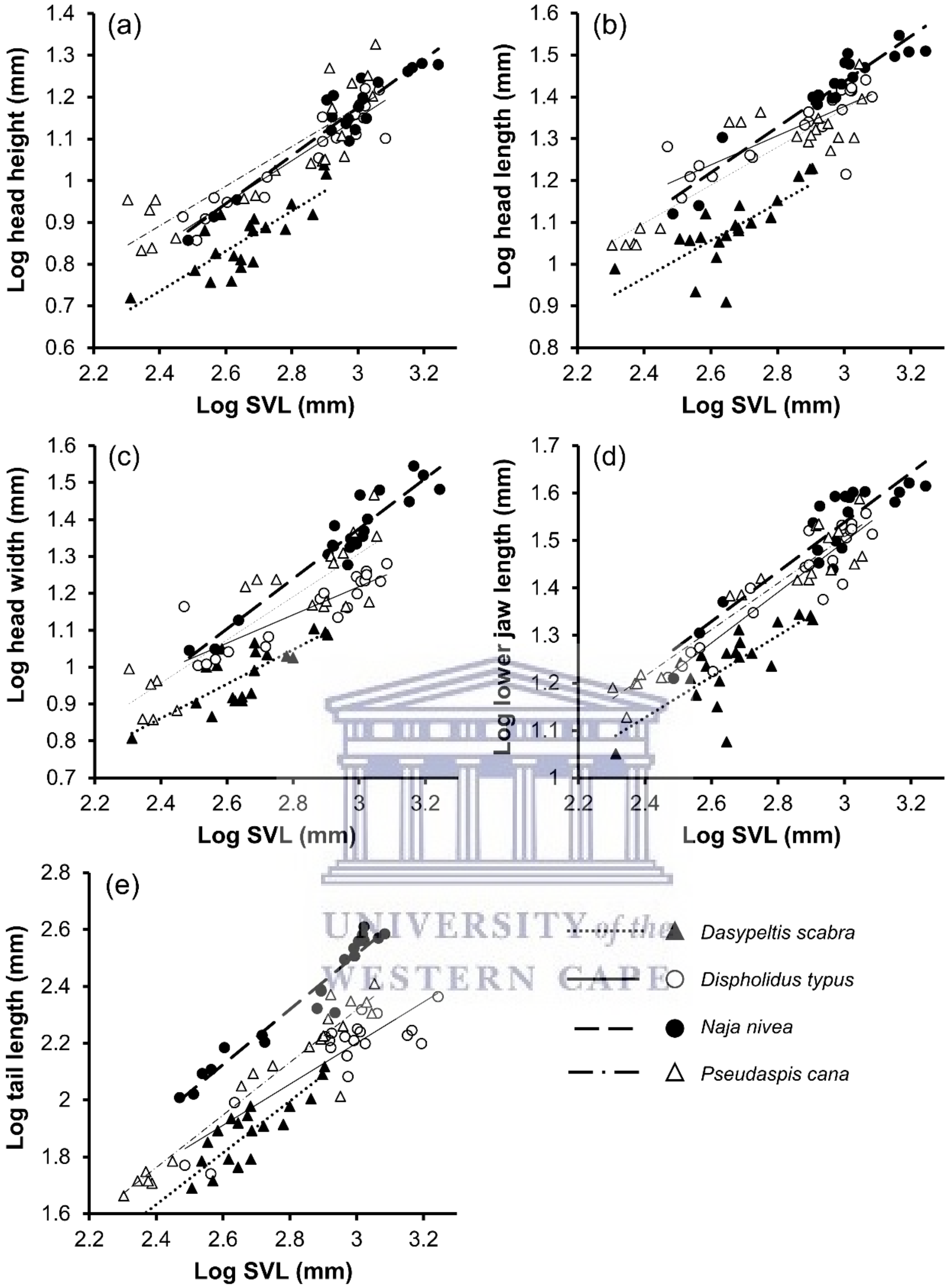

Fig. 7.3: Relationships between a) log head height, b) log head length, c) log head width, d) log lower jaw length, and e) log tail length relative to log SVL for *Dasypeltis scabra*, *Dispholidus typus*, *Naja nivea*, and *Pseudaspis cana* specimens measured in this study.

Table 7.1: Pairwise mean differences (p-values in parenthesis) for species-level comparisons of size-adjusted head measures, PC axes, and dietary niche breadths for four competing bird egg-eating snake species. Significant values in boldface.

Head height		*D. scabra*	*D. typus*	*N. nivea*
	D. scabra	-		
	D. typus	**0.056 (< 0.001)**	-	
	N. nivea	**0.070 (< 0.001)**	0.014 (0.368)	-
	P. cana	**0.061 (< 0.001)**	0.005 (0.999)	0.009 (0.999)

Head length		*D. scabra*	*D. typus*	*N. nivea*
	D. scabra	-		
	D. typus	**0.055 (< 0.001)**	-	
	N. nivea	**0.074 (< 0.001)**	**0.019 (0.048)**	-
	P. cana	**0.055 (< 0.001)**	0.001 (0.999)	0.018 (0.066)

Head width		*D. scabra*	*D. typus*	*N. nivea*
	D. scabra	-		
	D. typus	**0.035 (< 0.001)**	-	
	N. nivea	**0.090 (< 0.001)**	**0.055 (< 0.001)**	-
	P. cana	**0.063 (< 0.001)**	**0.028 (0.003)**	**0.027 (0.004)**

Lower jaw length		*D. scabra*	*D. typus*	*N. nivea*
	D. scabra	-		
	D. typus	**0.034 (< 0.001)**	-	
	N. nivea	**0.048 (< 0.001)**	0.014 (0.196)	-
	P. cana	**0.038 (< 0.001)**	0.004 (0.999)	0.009 (0.905)

PCA PC1		*D. scabra*	*D. typus*	*N. nivea*
	D. scabra	-		
	D. typus	**0.089 (< 0.001)**	-	
	N. nivea	**0.142 (< 0.001)**	**0.053 (0.001)**	-
	P. cana	**0.110 (< 0.001)**	0.020 (0.296)	**0.032 (0.017)**

Levin's BA		*D. scabra*	*D. typus*	*N. nivea*
	D. scabra	-		
	D. typus	**0.317 (< 0.001)**	-	
	N. nivea	**0.499 (< 0.001)**	**0.182 (< 0.001)**	-
	P. cana	**0.469 (< 0.001)**	**0.153 (< 0.001)**	**0.030 (< 0.001)**

7.4.4 Relationship between dietary niche and head morphology

Based on my examination of dietary data from the literature I estimated Levins' measure of niche breadth for the rhombic egg-eater as $B = 1.00$ (based on 31 feeding records; Bates & Little 2013), boomslang as $B = 2.91$ (based on 133 feeding records; Smith et al. 2019), cape cobra as $B = 4.00$ (based on 101 feeding records; Layloo et al. 2017), and mole snake as $B = 3.23$ (based on Dyer 1996; Underhill et al. 2009; and assorted feeding records from various literature and citizen science reports (Maritz & Maritz 2020), Table S7.6). I standardized these to $B_A = 0.00$ (rhombic egg-eater), $B_A = 0.32$ (boomslang), $B_A = 0.50$ (cape cobra), and $B_A = 0.47$ (mole snake) respectively (Fig. 7.4). I also calculated standardized Levin's B_A values for the expanded 34-taxon dataset (Table S7.6).

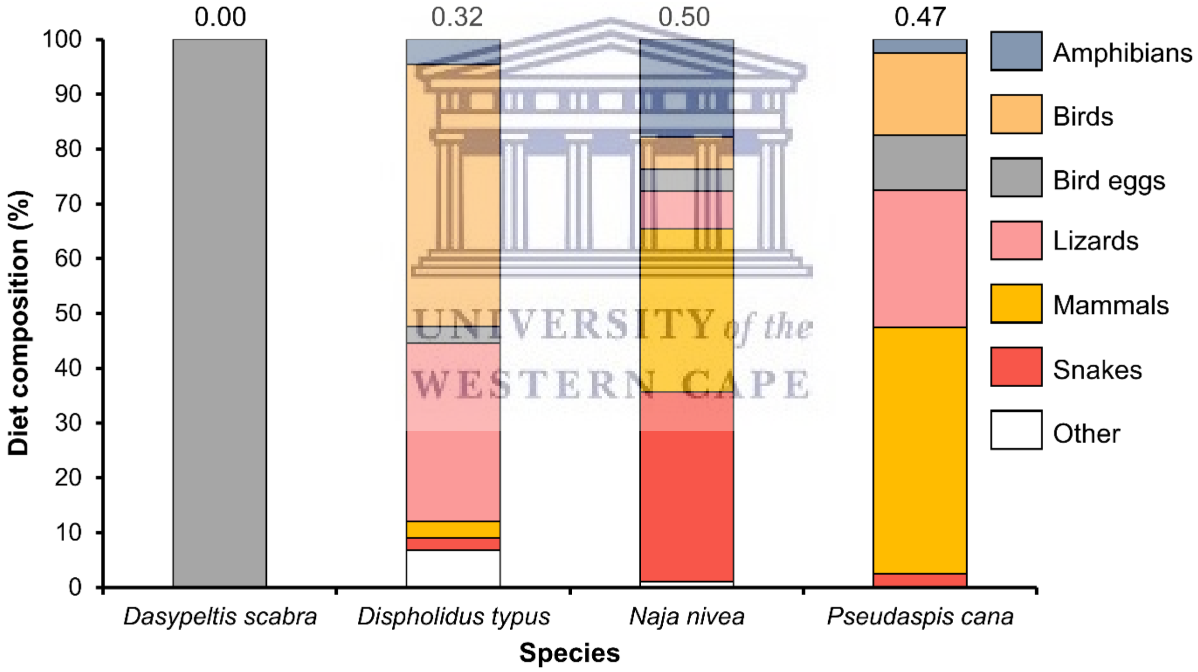

Fig. 7.4: Diet compositions as estimated from literature sources for *Dasypeltis scabra*, *Dispholidus typus*, *Naja nivea*, and *Pseudaspis cana*. Data labels above bars represent standardized measures of Levins' Niche Breadth (B_A).

I found similar results for non-phylogenetically and phylogenetically corrected regression analyses. In both analyses, I found a significant positive relationship between head sizes and dietary niche breadths across the four study species (non-phylogenetically corrected regression: $F_{1,\,3} = 28.426$, $P = 0.003$, $\beta = 0.259$, $R^2 = 0.93$; phylogenetically corrected regression: $F_{1,\,3} = 76.203$, $P = 0.013$, $\beta = 0.261$, $R^2 = 0.97$) when compared on their own. However, when compared across the expanded 34-taxon dataset, although the relationship remained significant, the correlation between these traits was drastically weaker ($F_{1,\,32} = 4.197$, $P = 0.048$, $\beta = 0.101$, $R^2 = 0.12$; Fig. 7.5). Overall, dietary specialist species tended to have smaller heads to dietary generalists.

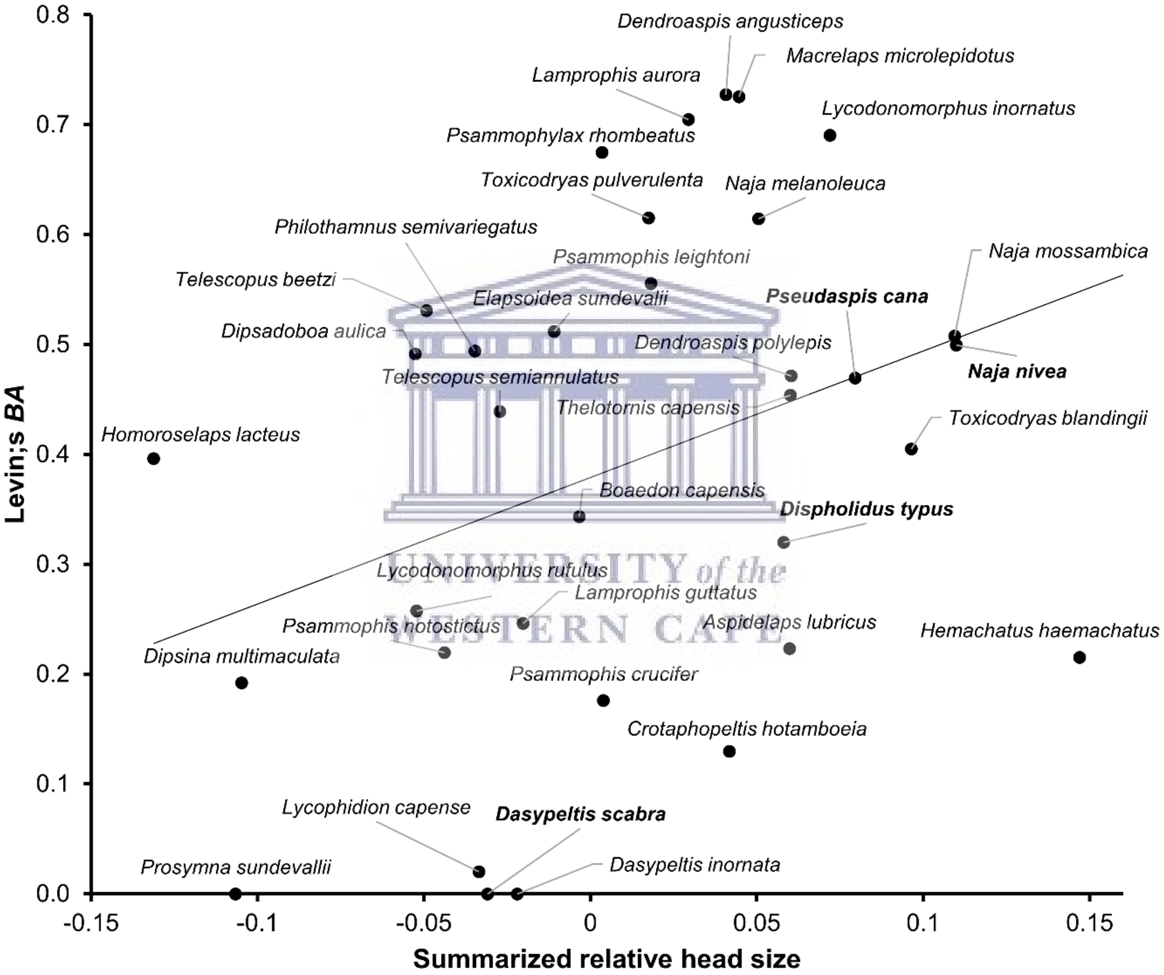

Fig. 7.5: Relationship between summarized head sizes derived from phylogenetic PCA, and Levins' standardized measures of niche breadth between 34 snake species. The four target species are highlighted in boldface.

7.5 Discussion

Contrary to my expectation, rhombic egg-eaters have significantly smaller heads relative to body size than competing boomslang, cape cobras, and mole snakes. I found evidence of a significant phylogenetic signal for head size across these taxa and their relatives, suggesting that the disparities in head shapes between them were not present as a result of head size being phylogenetically conserved and were instead derived, possibly as a result of variations in their respective diets. Relative to SVL, an average individual rhombic egg-eater has significantly smaller measures of head height, head length, head width, and lower jaw length than equivalently sized competitors in southern Africa. These differences in head size and shape were not affected by variances associated with sexual size dimorphism but were positively associated with dietary niche breadth to some degree, suggesting adaptive responses to feeding were likely selected for as these taxa evolved. Species with the largest heads had the broadest diets, the majority of which included bird eggs.

Dietary specialization in snakes is often associated with adaptive changes in functional morphology, typically in the feeding apparatus, relating to the specific prey type being consumed (Cundall & Greene 2000; King 2002; Hoso et al. 2007). Typically, snakes that have adapted to consume bulky, robust prey types possess long head and jaw elements and have relatively large gapes that allow them to efficiently exploit large prey (Arnold 1993; Jayne et al. 2018; Moon et al. 2019). Given the findings of de Queiroz & Rodríguez-Robles (2006) regarding the challenges of consuming bird eggs, I expected to find that specialist egg-eaters would have relatively large heads that allow them to compete with the absolutely larger heads of their large-bodied competitors, but this was not the case. Instead, I found that egg-eaters have smaller heads than other southern African snakes that facultatively eat bird eggs. Moreover, ancestral reconstruction of head size across this phylogeny showed that the large head sizes of facultative bird egg-eating species evolved from ancestors with smaller sized heads, but that this transition did not take place within the *Dasypeltis* lineage. The evolution of large head size in those species may therefore have resulted from a variety of environmental factors unrelated to the consumption of bird eggs.

Interspecific competition for food by snakes typically occurs between species that share similarities in their ecologies, morphologies, and ancestry (for examples see Luiselli 2006a; Luiselli 2008; Maritz et al. 2019). In *Dasypeltis,* the development of key phenotypical innovations and functional changes within their feeding apparatus allow these snakes to easily ingest bird eggs, a source of prey that most of their relatives are unable to consume. At present, egg-eaters do not compete with similarly sized closely related genera, like *Crotaphopeltis* or *Dipsadoboa,* and instead share and compete over food resources with phylogenetically distantly related species that morphologically differ from themselves in both absolute and relative morphology. Consequently, the specialized adaptations of egg-eaters, including their highly flexible jaw and neck tissue and vertebral hypapophyses (Gans 1952), allow for the decoupling of typical body-size constrained competition dynamics within at least some southern African snake communities. This represents a clear example of how the evolution of unique phenotypic traits can alter species interactions and community dynamics, the results of which can modify the relationship between phylogenetic distance and species interaction strength among dissimilar species within evolving meta-communities (Hunter 1998; Nascimento et al. 2011; Weber et al. 2017).

Competition between *Dasypeltis* and facultative bird egg-eating snakes in contemporary systems is potentially present as a consequence of historical competition amongst ancestral lineages, in line with the theory of the ghost of competition past (Connell 1980; Weber et al. 2017; Ye et al. 2019). Before adapting to exclusively feeding on bird eggs, ancestral *Dasypeltis* likely had a broader dietary niche (Barends & Maritz 2022b) and probably competed with several snake species of varying sizes. The transition towards bird egg specialization by *Dasypeltis* may have been selected in response to competition for non-avian prey by ancestral colubrids and other ecologically similar African snakes as a result of resource partitioning. If so, this divergence may have led to a reduction of competition for *Dasypeltis* by transitioning from a competitive network involving several small species of snakes to one comprised of fewer but larger snake species that greatly differ from *Dasypeltis* in their morphology and ecology.

Variation in the dietary compositions and the degree of dietary specialization versus generalization in snakes could explain the similarities and differences in head morphology between the facultative egg-eating snakes in my comparison (Arnold 1993; Greene 1997; Cundall & Greene 2000, Moon et al. 2019). Boomslang, cape cobras, and mole snakes each vary in their utilization of different prey resources, and these differences appear to conform with the disparities between their assorted head morphologies. Cape cobras occupied the most extreme position of morphological space in my analyses of head size covariation and had significantly larger head measures than boomslang and mole snakes respectively. Cape cobras have the broadest dietary niche of the four species but are primarily ophiophagous (Maritz et al. 2019). The consumption of robust, elongate prey types presents a unique set of mechanical challenges of ingestion not present in boomslang and mole snakes. Differences in head size between boomslang and mole snakes were less prominent, although mole snakes have wider heads, possibly reflecting their propensity for preying on mammals and adult birds (Maritz & Maritz 2020) whereas boomslang primarily consumes chicks, nestlings, and chameleons (Smith et al. 2019).

Field studies investigating competitive interactions between egg-eaters and their rivals are scarce, but laboratory-based experiments have shown that egg-eaters are extremely proficient at exploiting bird eggs despite their small body size. Gartner & Greene (2008) compared the feeding performance of *Dasypeltis* to a facultative bird egg-eating species from North

America, the common king snake, *Lampropeltis getula* and found that only large king snakes could consume small eggs while equivalently sized *Dasypeltis* showed much greater ingestion ability. Moreover, adult egg-eaters are likely able to consume up to 98% of eggs that they encounter across their range within southern Africa (Chapter 4). Egg-eaters may have therefore adapted towards a maximum head size optimum in congruence with the maximum sizes of available bird eggs which could potentially explain their small size. The apparent mismatch in egg-eater head size and bird egg-ingestion ability is largely achieved through the high degree of stretchability in the necks and jaws of these snakes, the limits of which require further investigation. A detailed examination of bird egg-eating performance and flexibility in gape size in egg-eater's direct competitors could provide further insight into competition for bird eggs between snakes in Africa.

For most snakes, head size is a major contributing factor towards determining the suite of prey that individuals can consume. However, several studies have shown that in some species, head morphology exhibits phenotypic plasticity in response to prey size and feeding opportunities. For example, Aubret et al. (2004) found that tiger snakes (*Notechis scutatus*) on mainland Australia have smaller heads than individuals from populations on nearby islands and attributed these differences to adaptive plasticity in response to differences in diet between those populations. Queral-Regil & King (1998) found that different feeding regimes affected head size development in North American water snakes (*Nerodia sipodon*). Similarly, Bonnet et al. (2001b) saw similar trends in head size development in captive Gaboon adders (*Bitis gabonica*) from Africa. Plasticity in head size in response to prey size does not appear to be present in all species of snakes (Forsman 1996; Schuett et al. 2005) and whether this is present in my study species requires clarification. Adult mole snakes vary in size from 1.4 m to 2 m, with individuals from the Western Cape being particularly large. Similarly, adult boomslang varies between 1.2 m and 2 m, and cape cobras vary between 1.4

m and 2.3 m (Alexander & Marais 2007). Whether these intraspecific differences in body size, and therefore also head size, manifest as a result of plastic responses to variable prey intake, are affected by environmental factors, or are entirely genetic is unclear.

Although prey size is a major factor in influencing head shape within most snakes (Arnold 1993; Cundall & Greene 2000; Jayne et al. 2018; Segall et al. 2020), the link between prey size and head size possibly only accounts for challenges relating to ingestion (Vincent et al. 2006). It is important to also consider other selective pressures that may have been involved in the evolution of head shape for different snake species. Factors such as habitat use, prey capture, and anti-predator defensive behaviour can play prominent roles in the evolution of the feeding apparatus and head sizes of many snake species (Hibbits & Fitzgerald 2005; Fabre et al. 2016; Segall et al. 2020). For example, the defensive display of *Dasypeltis* involves flattening and triangulation of their heads which they achieve by manipulating their quadrates (Young et al. 1999), a feature strongly associated with gape size (King 2002; Moon et al. 2019). However, while the evolution of head triangulation may have affected jaw structure and head size within *Dasypeltis,* it is thought to have evolved after their lineage adopted their dietary specialist lifestyles (Gans & Richmond 1957).

7.6 Conclusion

This study has important implications for understanding ecological interactions between competing snake species within and beyond the southern African region. My findings suggest that specialised morphology linked to feeding adaptations can decouple typical body-size constrained competition dynamics between sympatric snake species derived from ancient selective pressures. Competition for specific food resources between snake species may be present within dissimilar lineages today as a consequence of resource partitioning within evolving meta-communities. I suggest that to understand competition within contemporary snake communities, researchers should seek to also explore shifts in dietary niche utilization within extant snakes and their ancestors.

7.7 Acknowledgements

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Chapter 8: Summary and Conclusion

The goal of this thesis was to expand on the body of knowledge concerning the ecology of *Dasypeltis scabra* in the hopes that the information produced can be used to further our understanding of the importance of these snakes as predators in African ecosystems. Throughout the thesis, I sought to answer questions relating to the evolutionary origins and ecology of *D. scabra* to fill in important gaps in the knowledge of their lifestyles that may help to explain the functional roles of these snakes. Overall, the findings throughout my thesis show that *D. scabra*, and likely *Dasypeltis* in general, are unique among most snakes in their diet, feeding requirements, and feeding morphology, and thus potentially occupy a unique functional role in many ecosystems across Africa.

8.1 Avian oophagy by snakes and the evolution of bird egg specialization in *Dasypeltis*

Predation is among the most common causes of nest failure for birds and has major implications for avian ecology and life history strategies (DeGregorio et al. 2014). *Dasypeltis scabra* has been known to consume bird eggs for over a century (Smith 1849; Gans 1952; Bates & Little 2013) and several other snake species are also notable nest predators. In Chapter 2, I reviewed published and unpublished records of avian oophagy by snakes in an attempt to identify those species that eat bird eggs and discern global trends of these predation events. My review yielded few predation records ($N = 471$) across only 123 species of snakes (< 4% of all snakes) from 238 data sources, suggesting that most snakes do not eat bird eggs or at least have not yet been observed to do so. Snake species that consume eggs tend to be large-bodied, and most eggs consumed are generally small, emphasizing the morphological dynamics of egg consumption in snakes that likely exclude most species from utilizing these prey. Importantly, this study highlights biases in the publishing of feeding records and snake diet studies as many species that probably eat eggs could not be included in my list due to a lack of direct evidence.

Given the general rarity of snakes utilizing bird eggs as shown in Chapter 2, in Chapter 3 I investigated the evolutionary origins of egg specialization in *Dasypeltis*. The current diet of *Dasypeltis* appears to have originated from an ancestral generalist diet that initially included amphibians, birds, bird eggs, mammals, and reptiles. The shift towards bird egg exclusivity seemingly correlated with a shift in the African landscape from closed to open environments. Similar shifts in diet were observed in closely related African taxa such as *Crotaphopeltis* and *Dipsadoboa* (amphibian specialization), and *Telescopus semiannulatus* (reptile specialization). Other closely related taxa that did not experience major habitat shifts (for example *Toxicodryas* and most of the Asian genera within this clade) retained the ancestral generalist diet. Moreover, the dietary specialist genera evolved smaller body sizes than their generalist relatives. I suggest that increased competition for food and resultant resource partitioning likely occurred as habitat shifted and affected prey availability, which likely led to the evolution of specialised diets in these snakes.

8.2 Food availability and feeding requirements

Top-down predation by snakes can influence ecosystems indirectly by impacting prey populations. Predation by *Dasypeltis scabra* on the eggs of southern African birds has been documented on a few occasions (reviewed by Bates & Little 2013), and these snakes are regarded as the primary predatory threat to bird breeding success in the region. These snakes are therefore potentially modulating the recruitment of several ecologically important bird species. However, these snakes are currently only known to eat the eggs of 40 species of birds. This number is likely to greatly differ in reality given the high richness of birds that breed in southern Africa (720 species, Tarboton 2011). In Chapter 4, I investigated the ingestion ability of a colony of captive *D. scabra* to determine the suite of bird species that constitute potential prey for differently sized snakes. Adult snakes readily consume small and bulky eggs and can feasibly consume up to 98% (708 species) of eggs encountered across southern Africa. Contrastingly, juveniles can consume up to 50% (363 species) of eggs. This suggests that the eggs of nearly the entire range of southern African nesting birds are potential prey for *D. scabra*.

In Chapter 5, I investigated the minimum food intake required for *Dasypeltis scabra* to maintain yearly body condition. On average, *D. scabra* only requires meals equating to a remarkably low 61% of initial body mass to maintain that mass annually under captive conditions. Although this requirement is likely to be higher for wild snakes, these findings suggest that individuals could feasibly survive and grow by consuming just a handful of suitably sized eggs each year. Taken together with the results of Chapter 4, these findings suggest that *D. scabra* likely has access to a wide range of prey but does not require much food each year. However, bird breeding in southern Africa is seasonal (eggs are abundant in warmer months and are largely absent in colder months) and so snakes in the region likely only feed in late spring or summer and fast during winter. Feeding data of captive snakes showed that *D. scabra* appetite is highest when egg-laying peaks in October and greatly diminishes when egg-laying decreases in May. It is thus likely that the low maintenance requirements of *Dasypeltis* evolved as snakes adapted to prolonged periods of fasting when eggs are not as abundant.

8.3 Population and community dynamics

In Chapter 6, I estimated the population density of *Dasypeltis scabra* at Koeberg Private Nature Reserve using a spatially explicit capture-recapture modelling approach. Model estimates suggest densities of between 5 and 8 individuals per hectare across the reserve.

Given the size of Koeberg Private Nature Reserve (2900 ha), by process of extrapolation, this could indicate that thousands of individual egg-eaters occupy the reserve. With such a large population, these snakes could thus be responsible for the removal of tens of thousands of eggs from Koeberg Private Nature Reserve each year. If correct, this would provide one of the first estimates of the impact that predation by *Dasypeltis scabra* can have on bird recruitment.

Competition for resources between sympatric snakes usually occurs between species that share similarities in their morphology or are closely related (Luiselli 2006a). However, the unique diet of *D. scabra* means these snakes do not compete for food with closely related species and instead compete with several large-bodied (> 2000 mm SVL) taxa. In Chapter 7, I examined and compared the feeding morphology of *Dasypeltis scabra* to three of their main competitors: boomslang (*Dispholidus typus*), Cape cobras (*Naja nivea*), and mole snakes (*Pseudaspis cana*). The body and head morphology of egg-eaters are smaller than their competitors both in terms of absolute measures as well as relative to body lengths. This study highlights how the unique morphology of egg-eaters decouples typical body size dynamics of competition in snakes as *D. scabra* of all sizes are likely competing with larger competitors.

Based on my findings presented throughout this thesis, I suggest that *Dasypeltis scabra* may have evolved an optimal body size. Firstly, results in Chapter 2 show that *Dasypeltis* evolved a maximum length of < 1000 mm from an ancestor that likely ranged between ~1500 – 2000 mm. However, despite this decrease in size over time, modern adult *D. scabra* can seemingly ingest nearly the entire range of available eggs where they occur. Theoretically, larger individuals of 1500 – 2000 mm would not gain access to a significant number of additional prey but would require more eggs per year to maintain annual body condition. Thus, exceeding 1000 mm does not appear to be favourable for snake fitness. In addition, the small body size of *D. scabra* probably allows these snakes to occur at relatively high densities that potentially allow them to outcompete their rivals through exploitative competition.

8.4 Future recommendations

The knowledge generated in my thesis contributes to the existing body of knowledge on *Dasypeltis scabra*, and more broadly African snakes. Together, this information can help to form a foundation upon which an understanding of how predation by *Dasypeltis scabra*, and other snakes, can influence ecosystems indirectly through their impacts on prey populations. However, much of the work performed here was laboratory and model-based and may not necessarily reflect real-world patterns of wild snakes. Further field studies are likely required before any definitive claims of the functional importance of these snakes can be made. One area of focus for future research could involve investigating the circannual activity patterns in wild *Dasypeltis scabra*, possibly with radio telemetry or other methods. Information on the monthly and annual movement patterns in *D. scabra* populations could provide insight into the foraging activity of these snakes in the wild necessary to quantify their predatory impacts on bird populations.

Secondly, the work I performed with captive snakes in the laboratory was not performed under fully controlled environmental conditions. Future research could seek to repeat my experiments in a more controlled setting in which temperature, humidity, and light conditions are maintained at constant levels throughout the study. If these variables are kept consistent, researchers could robustly test whether feeding and appetite in *Dasypeltis scabra* is intrinsically controlled by an endogenous “internal clock”. Answers to these and other questions could be vital to gaining a clearer understanding of how frequently *D. scabra* feed.

Lastly, more robust estimates of *Dasypeltis* population density across its range are needed. These snakes occur over a large geographic range spanning multiple countries and several habitats, and thus various populations are likely to differ in their abundance and density. The spatially-explicit capture-recapture approach I employed was limited by few captures and suffered in accuracy as a result. Future studies could use similar methods but my recommendation would be that any such study should sample frequently (for example once a week for a year) to ensure a robust dataset and therefore statistically strong model outputs.

Supplementary Material

The supplementary material referred to in this thesis consists of a variety of additional datasets, figures, tables, phylogenetic tress, and text. Some of these materials are not suitable for inclusion in an A4-sized pdf document. I have therefore opted to upload all supplementary material to http://Figshare.com where the files will be permanently stored and freely accessible. Supplementary files for each chapter can be downloaded here:

Chapter 2 - https://doi.org/10.6084/m9.figshare.19786765.v1

Chapter 3 - https://doi.org/10.6084/m9.figshare.19786786.v1

Chapter 4 - https://doi.org/10.6084/m9.figshare.19786798.v1

Chapter 5 - https://doi.org/10.6084/m9.figshare.19786804.v1

Chapter 7 - https://doi.org/10.6084/m9.figshare.19786813.v1

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