

**Southern African pythons (*Python natalensis*):
Diet, human perceptions, and persistence despite
anthropogenic factors**

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ABSTRACT

Throughout the world, biodiversity is facing declines for multiple reasons, including climate change, land transformation, and habitat loss. Many species are facing decline and extinction, with little known about their basic life cycles and behaviours. This is especially true of ectotherms because of the additional challenges and difficulties involved in studying animals that do not feed as regularly as endotherms and are not necessarily active every day, or are not always readily apparent when they are active. This study focused on the southern African python (*Python natalensis*), the largest snake on the southern African subcontinent, about which little is known. Some research has been conducted regarding their breeding behaviour, but little is known about their diet, social interactions, persistence, seasonal and temporal behaviour, or anthropogenic impacts, uses, or importance. The overall aim of this study was to assess the persistence of the southern African python in South Africa, determining the threats faced and establishing baseline information about their life history, as well as documenting their anthropogenic significance. A systematic literature review was conducted on the family Pythonidae, examining the work done on the various species worldwide and highlighting areas that could be focused on for the benefit of their conservation. We found that the vast majority of work has been conducted on individuals in captivity, which has negative consequences for the management and conservation of wild animals. Social media was used to establish a detailed list of species of mammals, birds, reptiles, and fish that southern African pythons have been recorded eating, as well as document several novel feeding behaviours, specifically scavenging, caudal luring, active hunting, and an ontogenetic shift in their diets as they age. An online questionnaire and in-person interviews were conducted to gather information about the South African people's perspectives on pythons, documenting a trend of positivity towards these snakes, while also highlighting misinformation, which was addressed in a bilingual educational poster. We assessed some of the cultural beliefs about these snakes, as well as some

of their applications and uses in traditional medicine practices. Finally, we compared the occurrence data of southern African pythons over a ten-year time period, in light of land-use change, to establish whether they are persisting, increasing, or decreasing in their distribution in KwaZulu-Natal. We found that they are persisting through much of their range; however, there are proportionally more records from within protected areas than outside of them. We also established that pythons favour savannah regions, with rainfall between 500 and 900 mm p.a., below 400 m.a.s.l., with median summer temperatures between 22 and 26°C and median winter temperatures above 12°C. Conservation and management recommendations are made.

PREFACE

The data described in this thesis were collected in KwaZulu-Natal, Republic of South Africa, from February 2023 to August 2025. Experimental work was carried out while registered in the School of Life Sciences, now the Discipline of Biological Sciences, School of Agriculture and Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof Colleen T. Downs.

This thesis, submitted for the degree of Doctor of Philosophy in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.



.....
Kirsty J Kyle

October 2025

I certify that the above statement is correct and as the candidate's supervisor I have approved this thesis for submission.



.....
Prof Colleen T. Downs

Supervisor

October 2025

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DECLARATION 1 - PLAGIARISM

I, Kirsty J Kyle, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

PUBLICATION 1- published in Journal for Nature Conservation

‘Great Snakes!’: A systematic literature review of the family Pythonidae, highlighting conservation concerns

KJ Kyle & CT Downs

Author contributions:

KJK conceived the paper with CTD. KJK collected and analysed data and wrote the paper. CTD contributed valuable comments to the manuscript.

PUBLICATION 2- published in African Zoology

Southern African python (*Python natalensis*) diet, using information gathered from social media and historical data

KJ Kyle & CT Downs

Author contributions:

KJK conceived the paper with CTD. KJK collected and analysed data and wrote the paper. CTD contributed valuable comments to the manuscript.

PUBLICATION 3- published in Journal of Ethnobiology and Ethnomedicine

Beautifully dangerous or dangerously beautiful: Indigenous knowledge and perceptions of southern African pythons (*Python natalensis*) in southern African rural and urban areas

KJ Kyle & CT Downs

Author contributions:

KJK conceived the paper with CTD. KJK collected and analysed data and wrote the paper.

CTD contributed valuable comments to the manuscript.

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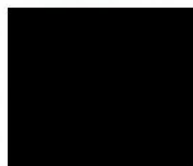
Protected and yet pressured: Persistence of southern African pythons (*Python natalensis*) in South Africa despite changing land use and other anthropogenic threats

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Author contributions:

KJK conceived the paper with CTD. KJK collected and analysed data and wrote the paper.

CTD contributed valuable comments to the manuscript.



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October 2025

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“I came that they may have life and life in abundance.” John 10:10



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look like, 3 = I'm not really confident, 4 = I'm not confident at all, they all look the same. For question 3, 1 = Absolutely deadly, one bite will kill me, 2 = They are very dangerous, if bitten I will get sick, but I won't die, 3 = I will get sick but will recover, 4 = They are harmless to humans. For question 4, 1 = Kill it immediately, 2 = Chase it away but not necessarily kill it, 3 = Ignore it completely, 4 = Encourage it to be there.)
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CHAPTER 1

INTRODUCTION

1.1 Background

Biodiversity loss is becoming an increasingly serious problem (Habibullah et al. 2022), with the primary drivers being agricultural expansion, climate change, marine exploitation, urbanisation, and invasive species (Hald-Mortensen 2023). A significant factor in biodiversity loss is the impact on ecosystem stability, which can potentially increase the risk of irreversible ecosystem collapse (Ives and Carpenter 2007; MacDougall et al. 2013). As Ellwanger et al. (2020) point out, the impacts of anthropogenic change on the environment reach far beyond biodiversity loss and climate change. It is not necessarily the loss of large, well-known species, but rather the loss of microorganisms, plants, and smaller animals, along with the ecosystem services they provide, that will impact our continued persistence (Ehrlich 1988).

Land use change, the primary driver of biodiversity loss (Davison et al. 2021), is believed to be responsible for endangering up to 85% of species at risk (Hald-Mortensen 2023). While some species can survive and even thrive in transformed habitats (Downs et al. 2021), there is typically a shift from specialist to generalist species (Concepcion et al. 2015), resulting in markedly reduced biodiversity and ecological richness (Downs et al. 2021). The loss of species at a local level has significant impacts on ecosystems (Hooper et al. 2012).

Presently, Africa and Asia have the fastest-expanding urban environments, with Africa expected to lead by 2050 (Kundu and Pandey 2020). These expansions will transform vast amounts of semi-rural and agricultural land surrounding cities (Chirisa 2008). The increasing human population will be largely dependent on natural resources for socioeconomic development, as well as its source of livelihoods (Achieng et al. 2023). Only 13% of the protected areas in the

biodiversity hotspots remain in Africa, with 13 countries on the continent predicted to become heavily urbanised by 2050 (Ayeeni et al. 2023). The African situation is further complicated by insufficient financial and technical support, as well as a lack of relevant data and information (Achieng et al. 2023). These are necessary to make informed decisions regarding land transformation and the resulting loss of biodiversity. Africa is predicted to be particularly vulnerable to climate change, with projected temperature increases of several degrees and an increase in extreme weather events, including flooding and droughts (Gemedu and Sima 2015). This, in turn, will have significant negative effects on biodiversity, food security, water availability and productivity levels in Africa (Hope 2009), increasing the pressure on already stretched natural resources.

While biodiversity is facing losses, the losses of terrestrial vertebrates are particularly high, with 32% of a large sample size (8,851/27,600 species) reported to be at risk in one study, accompanied by a decrease in population size and range (Ceballos et al. 2017). In addition to species extinctions, the world is experiencing broad, sweeping population declines and local extirpations in many taxa, which, in turn, have cascading consequences for ecosystem services and functioning (Ceballos et al. 2017).

The Global South is underrepresented in research (Hughes et al. 2023; Bars-Closel et al. 2024), particularly in relation to urbanisation and land transformation (Downs et al. 2021). Worldwide, 34 biodiversity hotspots have been identified, nine of which are on the African continent (Mittermeier 2004). Research has shown that, despite the Afrotropics experiencing the highest rates of deforestation globally, they are disproportionately the least well-researched biome (Deikumah et al. 2014).

While historical research has emphasised mammals, birds, and even amphibians, it is becoming apparent that population declines are being experienced throughout most vertebrate and invertebrate taxa (Roll et al. 2017). Evidence suggests that reptiles, including snakes, are declining worldwide (Gibbons et al. 2000; Reading et al. 2010). There are many factors leading to these reptile declines, most of which are interlinked and multifaceted, including habitat degradation and loss, environmental pollution, the introduction of invasive species, disease, unsustainable use and global climate change (Gibbons et al. 2000).

Mainland Africa is home to ~20% of the world's reptile species, yet it is poorly represented in herpetofaunal research, with significant knowledge gaps that impact effective species conservation (Tolley et al. 2016). While reptiles in many regions of Africa are poorly studied (Deikumah et al. 2014), southern and eastern Africa are considered better represented; however, even in these regions, significant gaps remain (Tolley et al. 2016). Herpetofauna are under particular threat because many have limited distributions, are sensitive to habitat transformation and are habitat specialists (Jenkins et al. 2014). Land transformation is identified as being the greatest threat to African reptiles (Tolley et al. 2016).

Concerning snakes in particular, they are considered one of the most challenging groups of vertebrates to accurately assess for declining populations (Reading et al. 2010). Their secretive habits and cryptic nature make them difficult to monitor, and the few long-term population studies that have been conducted have focused on North America, Europe and Australia (Matthews et al. 2002; Beebee et al 2009). Some of the drivers of snake population declines include habitat fragmentation and destruction, environmental degradation, fire, ecological succession, road mortality, climate change, disease and pathogens, chemical pollutants and toxins, trade, exploitation and the introduction of invasive alien species (Schmidt 2018).

1.2 Southern African pythons

Southern African pythons (*Python natalensis*) are the longest reptile in southern Africa, and arguably the largest in Africa (Alexander and Marais 2007; Marais and Kemp 2022). Originally the two large African pythons were considered one species, *Python sebae*, however, in 1999 *P. natalensis* was distinguished as a valid species (Broadley 1999). They are the only snake in southern Africa that grows large enough to possibly consider humans as prey; however, there are very few reports of this, although fatalities have been recorded (Branch and Haacke 1980; Branch 1998). They have historically been recorded reaching 6 m and weighing over 60 kgs; however, these massive specimens have most likely been largely exterminated, and very few over 5 m remain today (Branch 1998; Alexander and Marais 2007; Marais and Kemp 2022). They are largely active at night; however, they often spend time basking during the day, and occur in a wide range of habitats, avoiding true deserts and dense rainforests (Branch 1998). Many spend long periods submerged in water, even hunting from under the surface (Broadley 1983).

Pythons are generalist predators, feeding on a wide range of vertebrates, including birds, mammals, fish, and reptiles, and display a range of hunting techniques, which include caudal luring, scavenging, ambushing at water sources, and opportunistically feeding on birds' eggs (Kyle and Downs 2025). They are a long-lived species, living up to 27 years in captivity, with females capable of laying an ever-greater number of eggs as they grow larger (Branch 1998). Southern African pythons have a complex reproductive method, spanning periods of over six months from start to finish. A receptive female and multiple males interact and cohabit for lengthy periods, after which the female typically remains with her eggs until they hatch, and sometimes even for up to

three weeks after hatching. During this entire period, the female does not eat and loses significant body condition (Alexander 2018).

According to the IUCN listing, southern African pythons are ‘Least Concern’, although populations are known to be declining (Alexander and Tolley 2021). They are now extinct in parts of their range, e.g., the Eastern Cape; however, they are thought to have expanded in other areas (North-West, Gauteng, KwaZulu-Natal) and have recovered in areas where they were previously thought to be declining (Durban) (Tolley et al. 2023). Identified threats include habitat transformation, electrocution, roadkill, wanton killing, illegal harvesting for the pet and leather trade, food, and traditional medicine or *muthi* (Broadley 1983; Branch 1988; Alexander 1990; Beck 2009; Williams and Whiting 2016; Green et al. 2022). They are a protected species in the National Environmental Management: Biodiversity Act, 2004 (Act No. 10 of 2004): List of Terrestrial and Fresh Water Species (ToPS List) and are included in the CITES Appendix 11. Conservation recommendations for the species include quantifying their use in the *muthi* trade, population monitoring, and establishing their minimum area requirements, as well as minimum viable population sizes and geographic and prey requirements (Alexander and Tolley 2021; Tolley et al. 2023).

1.3 Study area

The southern African python has a distribution limited to central and southern Africa, including parts of South Africa, Botswana, Namibia, Zimbabwe, Zambia, Angola, Kenya, Malawi, Eswatini, Mozambique and Tanzania. As such, all locality records and observations documented during these studies originated from within this distribution. Each chapter focused on different topics and used data from distinct areas within this distribution. Chapter 2 is a literature review, which utilises

data from online sources worldwide, while Chapters 3, 4, and 5 employ sighting records from throughout the pythons' distribution to examine various aspects.

1.4 Problem statement

The southern African python (*Python natalensis*) is the largest snake in southern Africa, with both positive and negative anthropogenic significance. Python's prey preferences provide ecosystem services in agricultural areas (controlling problem animals), while also having negative impacts (consuming livestock). Pythons fill an important ecological niche, serving as both prey items and predators, and have managed to persist in large sections of their distribution despite facing multiple threats. Culturally, they hold a prominent place for many South Africans, and have economic significance through tourism, illegal trade in various forms, and a financial impact on livestock owners. Despite all of this, they are underrepresented in literature, with only six scientific papers written specifically about this species, mostly covering the details of their breeding behaviour. Due to their declining numbers trend and the lack of basic information about this keystone species, we endeavoured to retrieve basic information about southern African pythons, so that decision-makers and policymakers are better informed about this species and will, consequently, be better able to manage and conserve them widely.

1.5 Aims and objectives

The overall aim of this study was to assess the persistence of the southern African python in South Africa, determining the threats faced and establishing baseline information about their life history, as well as documenting their anthropogenic significance. Our objectives were:

1. To establish and list the literature and information already published about southern African pythons and the genus *Pythonidae*.
2. To determine the southern African pythons' diet and the hunting methods employed.
3. To establish the overall perceptions and attitudes towards pythons in KwaZulu-Natal and South Africa, what specific negative and positive beliefs are held about them, how informed the public is about them, and whether people are aware of the ecosystem services these snakes provide.
4. To establish if they are persisting in South Africa in the face of marked land transformation and what specific anthropogenic and natural threats they face.
5. To determine their environmental parameters and whether they are occurring and persisting within protected areas or public areas.

1.6 Structure of the thesis

The main body of this thesis is organised as manuscripts prepared for publication in peer-reviewed journal articles. The first chapter (Chapter 1) is the Introduction, which provides the literature review of the concepts covered in this study. The next four chapters (Chapters 2, 3, 4, and 5) are empirical chapters, each covering a specific objective. Each chapter is formatted according to the journal to which it has been submitted. Because of this thesis format, a certain degree of repetition, especially in the methods section, was unavoidable. However, this is deemed to be of little concern as this format allows the reader to read each chapter separately without losing the overall context of the thesis.

Chapter 2 was a systematic literature review of the reptile family Pythonidae, comprising 38 species across 11 genera. Chapter 3 investigated the southern African python's diet and feeding behaviours. We utilised historical data, anecdotal information from credible individuals, and data

collected from citizen science platforms (e.g., iNaturalist®) and social media platforms (e.g., Facebook®) to compile this list and gather the information. Chapter 4 detailed the results of a questionnaire conducted primarily in KwaZulu-Natal, inquiring about the attitudes and perceptions of the population towards southern African pythons. Chapter 5 investigated a dataset of southern African python locality records, which encompasses two time periods, before and after 2015. above 12°C. Chapter 6 is a general discussion as well as a summary of the findings, recommendations and conclusions.

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CHAPTER 2

‘Great Snakes!’: A systematic literature review of the family Pythonidae, highlighting conservation concerns

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Running header: Review of Pythonidae and conservation concerns

2.1 Abstract

Globally, many snake species are declining because of anthropogenic factors such as changing land use, illegal killing, unsustainable harvesting and poaching. Many of the larger snake species are particularly affected. The family *Pythonidae* consists of 38 species over 11 genera - many of which are relatively large in size. We conducted a systematic literature search using two search engines and found 512 peer-reviewed publications on members of the Pythonidae family. Since the first publication in 1844, scientific research on the family has increased steadily, with a major increase since 2000. The majority of these papers were focused on single species (84.7%) and focussed on snakes in captivity (60.1%). The most commonly researched species was *Python regius* (37.7%), followed by *Python bivittatus* (16.8%), and the most common topic researched was medical (30.3%), which encompassed studies on anatomy, development, medication, digestion, nutrition etc. The geographical areas where the most research has been conducted on pythons in their natural habitat were Australia and Oceania. While a relatively large amount of research has been conducted on this family, it is apparent that there is a strong bias towards captive-bred animals, and not enough research has been conducted on wild individuals. With the increasing anthropogenic pressures, this could lead to misinformed decisions in conservation efforts. We recommend that future work be conducted on these snakes in their natural environments to allow for informed decisions to be made for their protection. We also recommend that emphasis be placed on the species listed in the IUCN red data list as data deficient and the other species that are under-represented.

Keywords: Pythons, publications, snakes, reptiles, research.

2.2 Introduction

The suborder Serpentes encompasses all species presently described as snakes, and are distributed across every continent other than Antarctica in varying numbers (Uetz et al. 2024). They inhabit terrestrial and aquatic habitats, which range from temperate to tropical environments (Wallach et al. 2014). As of August 2024, 4,145 species of snakes have been described (Uetz et al. 2024). Globally, many snake species are declining because of anthropogenic factors such as changing land use, climate change, reduction in prey availability, illegal killing, unsustainable legal trade and poaching (Zipkin et al. 2020; Jolly et al. 2021; Santos et al. 2022); phenomena which particularly affect the larger bodied snakes (Hierink et al. 2020; Jolly et al. 2021).

The family Pythonidae consists of 38 species over 11 genera (Schleip 2008; Uetz et al. 2024). These snakes range from Africa, through India and Southeast Asia, into Oceania and Australia (Uetz et al. 2024). The earliest species of python was described in 1758 (then *Coluber molurus*, now *Python molurus*) by the father of scientific nomenclature himself, Linneaus (Uetz et al. 2024). There have been steady and consistent additions to the Pythonidae family over the centuries, with the most recent species (*Antaresia papuensis*) being described in 2021 (Esquerre et al. 2021). The Pythonidae is predominantly an Australian and South East Asian family, with only four of the 38 species occurring in Africa, four are from mainland Asia and the remaining 30 spread between Malaysia, Indonesia, Papua New Guinea, Australia and the surrounding islands (Uetz et al. 2024).

The Pythonidae include the largest snakes in the world (*Malayopython reticulatus*) (Murphy 2020) and feature prominently in the global wildlife trade. Many of these species are bred in captivity for either research, pet trade, leather, or meat industries (Luiselli et al. 2011). While the majority of python species (n = 19, 50%) are listed as Least Concern according to the

IUCN Red List, five are listed as Near Threatened, five as Vulnerable, and one as Endangered, four are listed as Data Deficient, and four have no information (IUCN 2024) (See Supplementary Information Table S2.1 for more details).

The objective of our review was to systematically assess the global research conducted and published on Pythonidae over the years and to identify trends to understand where the knowledge gaps are pertaining to this family. In particular, we evaluated whether this work has increased or decreased over time, determined which species were the most prevalent research subjects, established what topics the work focussed on and assessed if there were gaps in the research and where future research and resources should best be expended. As many python species are declining globally (IUCN 2024), we predicted that some of the factors causing this, such as anthropogenic land use change, killing, and poaching for personal consumption or trade (Hierink et al. 2020; D'Cruze et al. 2020), would be addressed in studies, especially in recent decades.

2.3. Methods

2.3.1 Data extraction

We performed an initial literature search using the search engine Scopus® using the keywords “Python” and “Serpentes”. The second word was added as there were complications because of the coding language, also called ‘Python’, which led to many false results when just the word “Python” was used. This was followed by a literature search using Google Scholar®, the duplicates were ignored, but it resulted in an additional 35 records. Following this, we conducted an individual Google Scholar® search using each species of python’s scientific name to pick up any publications we might have missed. These searches were conducted over the period 21st – 23rd May 2024. It included all publications up until May 2024. We then exported the data into an Excel®

spreadsheet, and manually sifted for accuracy and relevance. We sorted the data according to when the paper was published, which country the study originated from, what the topic of the study was, which species were involved, whether it was based on snakes in the wild or in captivity and whether it was a single species or multiple species study.

Any peer-reviewed, published papers that involved studies conducted on any of the members of the Pythonidae family were included in our review. Short communications, conference proceedings and notes that were published in peer-reviewed journals were also included. We excluded assessments, books and theses.

2.3.2 Classifications

We split the world's land masses into eight groups to better understand the distribution of the publications reviewed. These groups were Asia (27 countries), the Middle East, North Africa and Greater Arabia (23 countries), Europe (48 countries), North America (4 countries), Central America and the Caribbean (20 countries), South America (12 countries), Sub-Saharan Africa (48 countries) and finally Australia and Oceania (15 countries) (Rosenberg 2019) (see Supplementary Information Table S2.2 for more information).

We selected the topic by examining the title, keywords and abstract, and where necessary, more sections of the paper were read. Classifying the topics of the studies was difficult as many studies spanned more than one topic, and some were general, vague or inconclusive; in cases where more than one topic was covered, the main topic was selected. The classification “medical” was used for studies where snakes were used as study animals for experiments, clinical trials for medication, and exploration of snake physiology. This was done because it was difficult to

differentiate between topics at a finer scale, and having more categories made the data more clumsy and complicated to work with.

2.3.3 Statistical analyses

We used descriptive statistics to summarise the data and establish trends and frequencies. We used Chi², Goodness of fit and Kruskal-Wallis to determine significant trends. The statistical tests were performed using base R (R Core Team, 2024). We created word clouds to summarise some of the data using base R (R Core Team, 2024).

2.4 Results

Our searches revealed 559 possible papers for inclusion, which, once irrelevant papers and publications were excluded, were reduced to 512 (Supplementary Information Table S2.3). This resulted in a data set focusing on many different aspects of members of the Pythonidae family (Fig. 2.1).

Of the 38 snake species within the python genus, only 23 have been the main feature of scientific papers. Of the 15 species that have not been researched, according to the IUCN Red Listing as of December 2024, three are listed as Data Deficient, four are listed as Vulnerable, four are of Least Concern, one is Near Threatened, and three are not listed (Fig. 2.2).

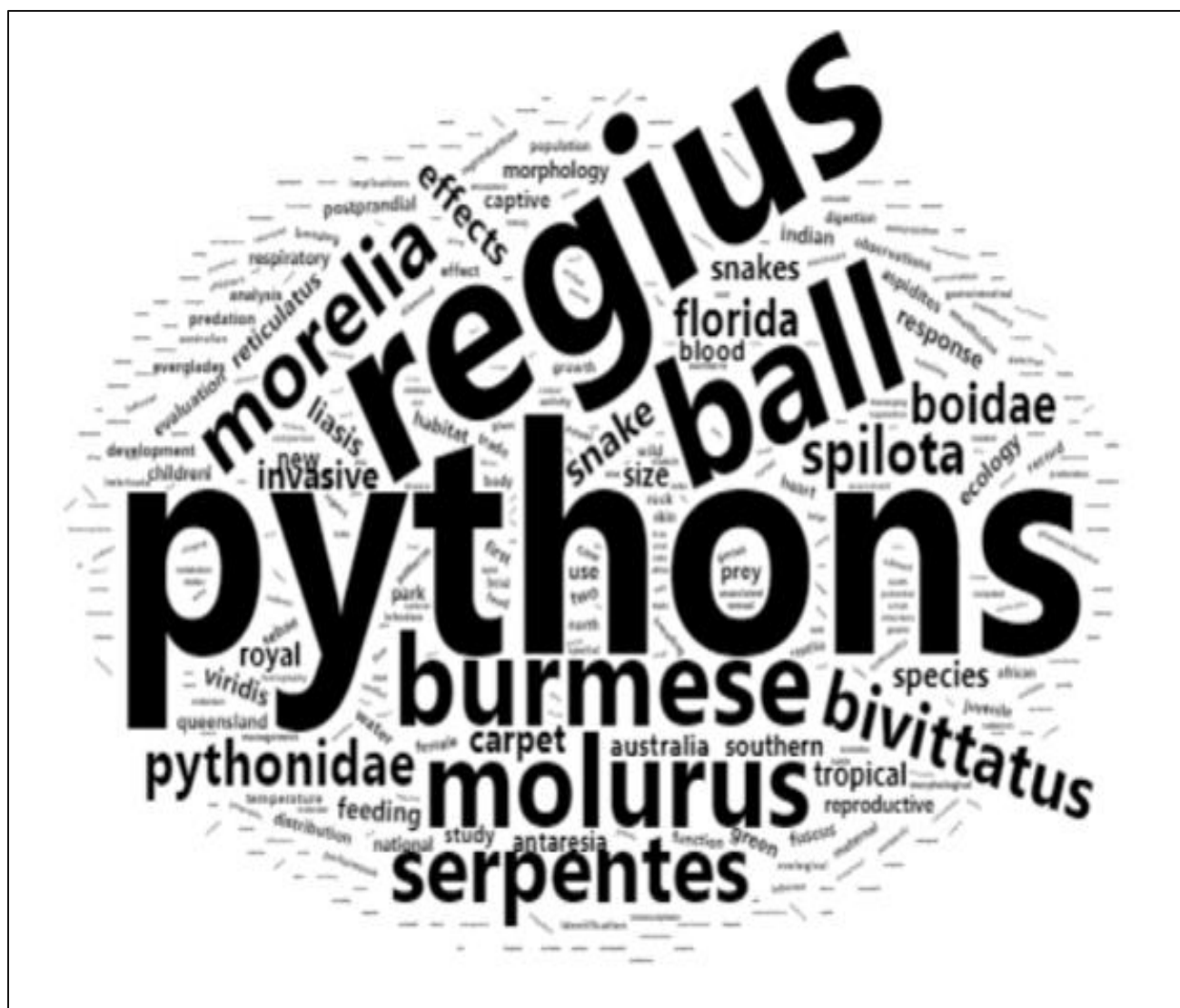


Figure 2.1: A word cloud created using the titles of the papers detailed in this global systematic review, with the size of the words indicating the number of times each word was used, with the larger words used more often than the smaller words.

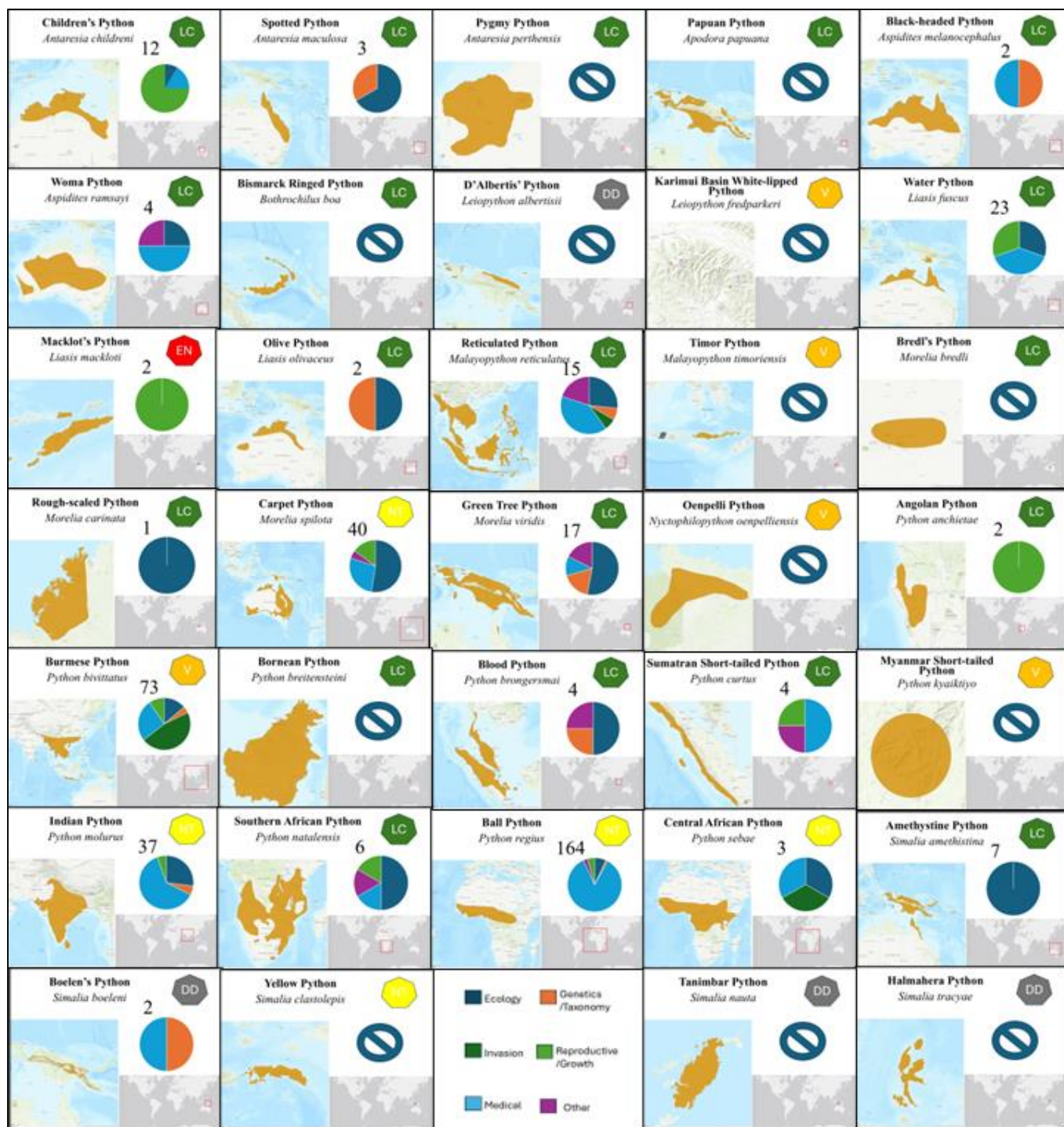


Figure 2.2: The 34 species of python listed by the IUCN in the family Pythonidae, with their IUCN Red Listing (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered), geographic range (Source: IUCN), number of publications found during the literature search up

until May 2024, and a pie chart with the proportion of publications using six broad study topics (colour legend).

2.4.1 Number of publications with time

Globally, the first scientific publication on a python species that we could find was an account of Thomas Savage's observations of *Python natalensis* in 1844, published in the Journal of Natural History. All the snakes mentioned in this paper were killed on sight as 'threats to man and beast' in the former colonies that form present-day South Africa (Savage, 1844). There was a significant difference in the number of publications over the decades (chi-squared = 743.15, df = 8, p-value < 0.05, Fig. 2.3). Research publications on pythons were slow to start, with only five being published up until 1971. The next decade showed an increase, with 17 papers being published, and over the decades preceding today, they have increased steadily, with a significant increment at the turn of the century. The data showed that research on pythons has increased dramatically since 2000, with 54 publications between 1991 and 2000, 138 from 2001 to 2010, and 211 between 2011 and 2020. Over 53% of the total publications have been published since 2011 (Fig. 2.3).

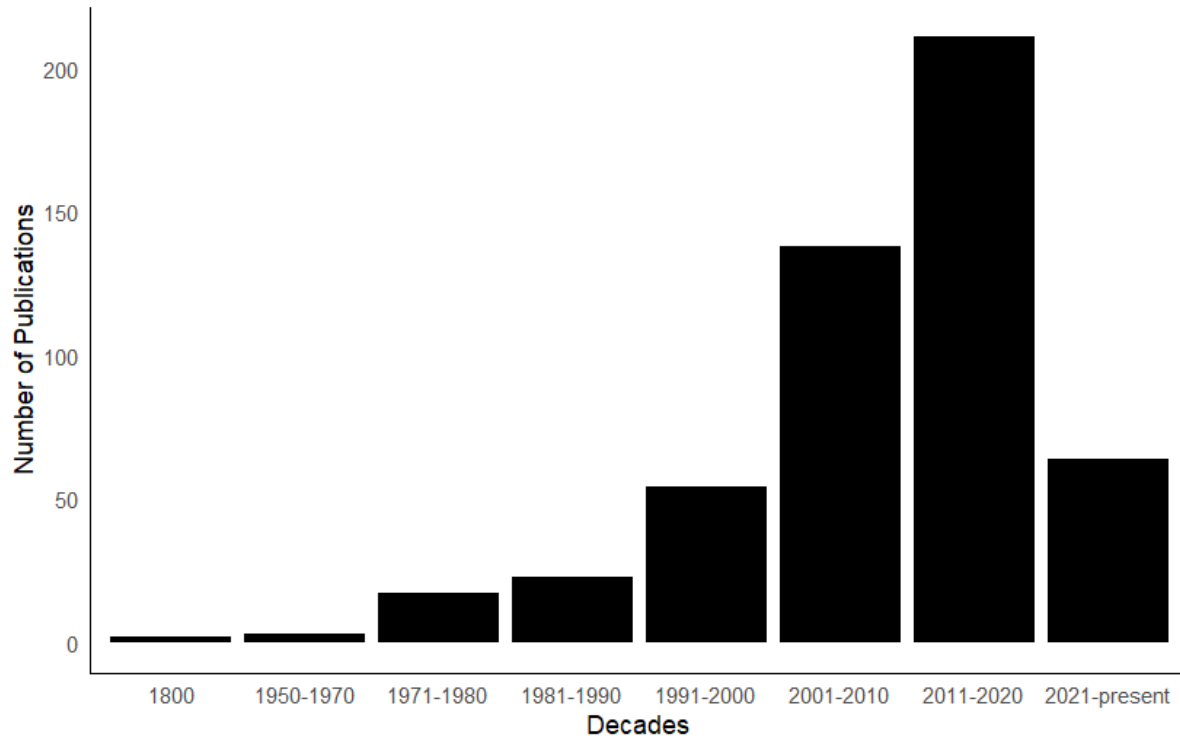


Figure 2.3: Distribution of the "python" papers over the decades from the 1800s to the present day following our systematic review.

When we consider the topics of the published papers before and after the turn of the 21st century, it is interesting to note how much more evenly spread the research efforts were in the past (Table 2.1). While medical research has always dominated python studies, historically, there were other topics which shared the main attention, including reproduction, morphology and behavioural studies, with medical topics accounting for 25% of the publications. In recent years, medical research has accounted for nearly half of the publications, while the second highest category is invasive research, which was not even featured before 2000 (Table 2.1).

Table 2.1: Changes in the distribution of different topics of python research over time.

Topic	1800 - 2000		2001- Present	
	No.	%	No	%
Anthropogenic			1	0.2
Behaviour	9	9.1	16	3.9
Capture			1	0.2
Colouration	2	2.0	5	1.2
Disease	4	4.0	15	3.6
Distribution/Movement	6	6.1	19	4.6
Ecology	4	4.0	16	3.9
Feeding	7	7.1	19	4.6
Genetics	2	2.0	17	4.1
Invasion			42	10.2
Medical	24	24.2	170	41.2
Morphology	8	8.1	5	1.2
Parasite	4	4.0	21	5.1
Prehistoric			2	0.5
Reproduction	20	20.2	27	6.5
Review	2	2.0	6	1.5
Size	4	4.0	7	1.7
Taxonomy	1	1.0	4	1.0
Threat			2	0.5
Trade	2	2.0	18	4.4
Total	99		413	

Historically, more emphasis was placed on research conducted on non-captive specimens, but post-2000, the research has predominantly been conducted on specimens in controlled environments (Table 2.2). Once again, we notice the sudden advent of invasive species research after 2000, further reducing the percentage of work performed on specimens in their natural

habitat. Most of the work was on captive animals ($n = 284/512$, 55.4%). In comparison, wild animals accounted for 28.1% of the papers ($n = 144/512$), and cases where work was conducted on invasive pythons contributed 8.4% of the papers ($n = 43/512$). There were 40 papers where the status of the snakes studied was unclear, as the authors did not clarify if the work was done in captivity, on wild occurring snakes or on snakes that were invasive to the area (Table 2.2).

Table 2.2: Comparison of the research pre- and post-2000 in relation to wild-living and captive studies on python species.

Status	1800 - 2000		2001- Present	
	Number	%	Number	%
Both	1	1.0		
Captive	47	47.5	237	57.4
Wild	32	32.3	112	27.1
Invasive			43	10.4
Unclear	19	19.2	21	5.1
	99		413	

2.4.2 Geographical distribution of python studies

We examined the type of studies in relation to where they were conducted geographically. Less than half ($n = 210/512$; 41%) of the studies mentioned where they took place; however, those relating to invasive species and the pet trade, as well as those involving wild specimens, included this information more frequently than the other topics. The number of python papers differed significantly according to world land mass region (X-squared = 201.6, $df = 6$, $p < 0.05$); most

studies on pythons were conducted in Australia and Oceania, with 78 of the 91 papers being focused primarily on Australia, five included multiple countries, six were from New Guinea, and two were from Papua New Guinea (Table 2.3). The next highest grouping was North America, with 46 papers; 37 of those were in Florida, United States of America (USA), where *P. bivittatus* and *P. sebae* have invaded the Everglades National Park (Table 2.3). Central America and the Caribbean had no records, and the Middle East, North Africa and Greater Arabia had only one study (Table 2.3).

Table 2.3: Details of the geographical distribution of the python papers assessed.

Geographical region	Count of countries	Sum of papers
Asia	12	34
Australia and Oceania	3	91
Europe	6	7
Middle East, North Africa and Greater Arabia	1	1
North America	1	46
South America	2	4
Sub-Saharan Africa	8	27

2.4.3 Single or multiple species and topics of studies

We examined the types of studies and whether they focused on single or multiple species and found that 85% (435/512) of them were single-species studies. The most frequently studied species was *Python regius*, accounting for 37.7% (164/435) of the total papers. This was followed by *P. bivittatus* with 16.8% (73/435), and *Morelia spilota* with 9.2% (40/435) of the papers.

Interestingly, the topics covered did not reflect the same situation, with *P. regius* covering the most topics (n = 12, 60%), followed by *P. molurus* with 11, and *M. reticulatus* having research covering ten topics (Table 2.4).

The species most frequently studied in the multiple species papers was *Python regius*, accounting for 23 of the 65 species/studies mentioned. This was followed by *P. bivittatus* with 16, and *P. molurus* and *M. reticulatus* with nine and seven accounts, respectively. Thirteen of these papers only mentioned the genus that had been studied, and this was dominated by the genus *Python*, followed by *Leiopython*. Of these multiple-species papers, 38 were conducted on snakes in captivity, five involved invasive snakes, and 17 were species in the wild, while 19 did not mention the status of the snakes.

Table 2.4: List of python species, the number of topics covered, the number of papers published and the percentage of the total number of papers in this review.

Species	Number of topics	Number of papers	Percentage of total (%)
<i>Antaresia childreni</i>	3	12	2.8
<i>Antaresia maculosa</i>	3	3	0.7
<i>Apodora papuana</i>	2	2	0.5
<i>Aspidites melanocephalus</i>	4	6	1.4
<i>Aspidites ramsayi</i>	3	4	0.9
<i>Liasis fuscus</i>	6	23	5.3
<i>Liasis mackloti</i>	1	2	0.5
<i>Liasis olivaceus</i>	2	2	0.5
<i>Malayopython reticulatus</i>	10	15	3.5
<i>Morelia carinata</i>	1	1	0.2
<i>Morelia spilota</i>	9	40	9.3
<i>Morelia viridis</i>	8	17	3.9
<i>Python anchietae</i>	1	2	0.5
<i>Python bivittatus</i>	10	73	16.9
<i>Python brongersmai</i>	3	4	0.9
<i>Python curtus</i>	3	4	0.9
<i>Python molurus</i>	11	37	8.6
<i>Python natalensis</i>	5	6	1.4
<i>Python regius</i>	12	164	38.0
<i>Python sebae</i>	3	3	0.7
<i>Simalia amethystina</i>	4	7	1.6
<i>Simalia boeleni</i>	2	2	0.5
<i>Simalia kinghorni</i>	2	3	0.7

2.4.4 Journals

The papers that we assessed on python species were published in a range of different journals and other publications ($n = 485$). Most papers were published in the Journal of Experimental Biology ($n = 21$, 4.1%). Next was the Journal of Herpetology, with 15 (2.9%). The mean number of publications per journal was two.

2.5 Discussion

Our review data indicate that research on pythons has increased since the turn of the century, with a corresponding rise in both the topics covered and the species studied over time. Concerning snakes living in the wild or in captivity, there has been an increase in both. The first invasive snake studies were two conducted in 2008, followed by one in 2010, after which they increased rapidly.

There is an abundance of literature supporting the fact that snakes in the wild are a challenging group to work with (McCann 2007; Durso et al. 2011; Miranda et al. 2013). This likely explained the prevalence of studies using captive specimens rather than wild snakes. As many python species are commercially farmed, either for the pet, leather, research or meat trade, they are an easily available commodity as research models. Many studies conducted on captive specimens are believed to still hold value in relation to the wild populations of these snakes, as topics such as anatomy, disease, and response to medication are applicable to specimens across the board, whether they are captive-bred or in their natural habitat. Behaviour studies may be a different matter, as there is literature supporting that behaviours observed in captivity are relevant to animals in the wild (Neill 1960), as well as literature stating that behaviour in captivity differs from that in the wild (Warwick et al. 2013).

Ironically, in the case of the Burmese python, *P. bivittatus*, which the IUCN lists as a Vulnerable species (IUCN 2024), considerably more work has been done on them as an invasive species in Florida than in their native habitats. Of the 90 papers that included work on *P. bivittatus*, either specifically or in a multiple species study, only eight were conducted on specimens in their native habitat, 36 involved captive animals, and 40 were related to their invasion of the Everglades, USA. For six studies, it was unclear whether they examined wild, captive or invasive python species. This suggests that although a species may be well-represented in the scientific literature, it does not necessarily mean that enough is known to effectively conserve it in its native wild habitats. *Python regius* is another good example, with 172 papers published on them in captivity, and only 11 in the wild.

It is essential to note that this systematic review only examined scientific, peer-reviewed publications; however, there will likely be many non-scientific publications and articles that may also make important contributions and cover a range of topics. At a later date, it would be beneficial to analyse these publications and see if similar trends are reflected here. It is also noteworthy that some IUCN-listed animals have been evaluated despite a scarcity of published scientific information on them. This review intentionally excluded assessments, which could account for some of the information that would be used for these evaluations, as well as other methodologies that can be applied when available research is limited.

Identifying the geographic location of the studies proved difficult, as most publications did not expressly say where the study had taken place. Most of the studies on snakes in the wild described their study area, but because of the prevalence of studies using captive-bred snakes, it was difficult to establish where the study was conducted. Some studies also involved snakes from

several different areas or countries; for example, the pythons from Indonesia and Australia were often studied together.

Of the three geographical areas where pythons occur naturally, Australia and Oceania were most represented for the work on python species living in the wild, with 80 studies published, compared with 28 for Asia and 17 for sub-Saharan Africa. The lack of other top predators and large mammalian species may account for this, with more attention being given to large snakes because of their role as apex predators in Australia (Fearn et al. 2005; Sutherland and Bryant 2014). In contrast, many more mammals in Asia and Africa would draw attention and funding first (Kabelik and Hofman 2018).

Outside of Australia and Oceania, North America had the highest number of publications, with 46; however, 39 focused on the invasion of the Everglades. Unfortunately, considerably more work is being conducted on these snakes as invasive species than on understanding them to protect them in their natural habitat. The number of species that lack research is concerning ($n = 14$), including those with little research ($n = 13$ with fewer than five publications), especially in non-captive situations. Surprisingly, little work has been conducted on pythons, considering the important role they play ecologically as both predators and prey, culturally, as they feature extensively in many different religions and cultures, and economically, as both wild-caught animals and captive-bred animals. Studies highlight the importance of snakes, and particularly pythons, in both the bushmeat and the skin trade, drawing attention to the fact that much of this trade is unregulated and unmonitored (Eniang and Ijeomah 2011; Jensen 2017). As such, some species may be in a more serious situation than is thought. *Python natalensis*, for example, is presently listed as least concern; however, the suggested conservation interventions are to establish the extent to which these snakes are being harvested in the wild for the traditional medicine trade

in southern Africa (Tolley et al. 2023). As such, this unmonitored trade could pose a significant problem for many of these species on an unknown scale and is an area that warrants urgent investment in research efforts.

As many python species are declining globally (IUCN 2024), we predicted that some factors contributing to this decline, such as anthropogenic land use change, killing, and poaching for meat or trade, would be better addressed. However, although the number of studies on python species has increased dramatically in recent years, there remains a paucity of studies providing management recommendations to prevent the loss of threatened python species. This area warrants urgent attention, especially in light of climate change and habitat loss, which are significant threats to pythons.

CRedit authorship contribution statement

Kirsty Kyle: Writing – original draft, Validation, Methodology, Formal analyses, Conceptualisation, Data curation. **Colleen T. Downs:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualisation.

Declaration of competing interest

The authors have no competing interests.

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2.9 Supplementary information

Supplementary information Table S2.1. Python species and their Red List status.

Species	Common name	Described	Red List Status	Date of listing
<i>Antaresia childreni</i>	Children's python	1842	Least concern	2017
<i>Antaresia maculosa</i>	Spotted python	1873	Least concern	2017
<i>Antaresia papuensis</i>	Papuan spotted python	2021		
<i>Antaresia perthensis</i>	Pygmy python	1932	Least concern	2017
<i>Apodora papuana</i>	Papuan python	1993	Least concern	2014
<i>Aspidites melanocephalus</i>	Black-headed python	1864	Least concern	2017
<i>Aspidites ramsayi</i>	Woma python	1882	Least concern	2017
<i>Bothrochilus boa</i>	Bismarck ringed python	1843	Least concern	2011
<i>Leiopython albertisii</i>	D'Albertis' python	1878	Data deficient	2014
<i>Leiopython fredparkeri</i>	Karimui Basin white-lipped python	2014	Vulnerable	2014
<i>Liasis fuscus</i>	Water python	1873	Least concern	2017
<i>Liasis mackloti</i>	Macklot's python	1844	Endangered	2019
<i>Liasis olivasceus</i>	Olive python	1842	Least concern	2017
<i>Malayopython reticulatus</i>	Reticulated python	1801	Least concern	2011
<i>Malayopython timoriensis</i>	Timor python	1876	Vulnerable	2019
<i>Morelia azurea</i>	Northern green tree python	1874		
<i>Morelia bredli</i>	Bredl's python	1981	Least concern	2017
<i>Morelia carinata</i>	Rough-scaled python	1981	Least concern	2017
<i>Morelia imbricata</i>	Southwestern carpet python	1981		
<i>Morelia spilota</i>	Carpet/diamond python	1804	Near threatened	2017
<i>Morelia viridis</i>	Green tree python	1872	Least concern	2017
<i>Nyctophilopython</i>				2017
<i>oenpelliensis</i>	Oenpelli python	1977	Vulnerable	
<i>Python anchietae</i>	Angolan python	1887	Least concern	2019

<i>Python bivittatus</i>	Burmese python	1820	Vulnerable	2011
<i>Python breitensteini</i>	Bornean python	1881	Least concern	2011
<i>Python brongersmai</i>	Blood python	1938	Least concern	2011
<i>Python curtus</i>	Sumatran short-tailed python	1872	Least concern	2012
<i>Python kyaiktiyo</i>	Myanmar short-tailed python	2003	Vulnerable	2011
<i>Python molurus</i>	Indian python	1758	Near threatened	2019
<i>Python natalensis</i>	Southern African rock python	1833	Least concern	2019
<i>Python regius</i>	Ball python	1802	Near threatened	2020
<i>Python sebae</i>	Central African python	1788	Near threatened	2019
<i>Simalia amethystina</i>	Amethystine python	1801	Least concern	2013
<i>Simalia boeleni</i>	Boelen's python	1953	Data deficient	2014
<i>Simalia clastolepis</i>	Yellow python	2000	Near threatened	2019
<i>Simalia kinghorni</i>	Scrub python	1933	Least concern	
<i>Simalia nauta</i>	Tanimbar python	2000	Data deficient	2019
<i>Simalia tracyae</i>	Halmahera python	2000	Data deficient	2019

Supplementary information Table S2.2. Geographic regions and the countries included in them (Rosenberg, 2019)

Geographic regions and the countries included in them.							
Asia	Middle East, North Africa and Greater Arabia	Europe	North America	Central America and the Caribbean	South America	Sub-Saharan Africa	Australia and Oceania
Bangladesh	Afghanistan	Albania	Canada	Antigua and Barbuda	Argentina	Angola	Australia
Bhutan	Algeria	Andorra	Greenland	The Bahamas	Bolivia	Benin	East Timor
Brunei	Azerbaijan	Armenia	Mexico	Barbados	Brazil	Botswana	Fiji
			The United States of America				
Cambodia	Bahrain	Austria		Belize	Chile	Burkina Faso	Kiribati
China	Egypt	Belarus		Costa Rica	Colombia	Burundi	Marshall Islands
							The Federated States of Micronesia
India	Iran	Belgium		Cuba	Ecuador	Cameroon	
Indonesia	Iraq	Bosnia and Herzegovina		Dominica	Guyana	Cape Verde	Nauru
Japan	Israel	Bulgaria		Dominican Republic	Paraguay	The Central African Republic	New Zealand
Kazakhstan	Jordan	Croatia		El Salvador	Peru	Chad	Palau
North Korea	Kuwait	Cyprus		Grenada	Suriname	Comoros	Papua New Guinea
		Czech Republic					
South Korea	Lebanon			Guatemala	Uruguay	Republic of the Congo	Samoa
						The Democratic Republic of the Congo	
Kyrgyzstan	Libya	Denmark		Haiti	Venezuela	Cote d'Ivoire	Solomon Islands
Laos	Morocco	Estonia		Honduras		Djibouti	Tonga
Malaysia	Oman	Finland		Jamaica		Equatorial Guinea	Tuvalu
Maldives	Pakistan	France		Nicaragua		Eritrea	Vanuatu
Mongolia	Qatar	Georgia		Panama		Ethiopia	
Myanmar	Saudi Arabia	Germany		Saint Kitts and Nevis			

Nepal	Somalia	Greece	Saint Lucia	Gabon
Philippines	Syria	Hungary	Saint Vincent and the Grenadines	The Gambia
Singapore	Tunisia	Iceland	Trinidad and Tobago	Ghana
Sri Lanka	Turkey	Ireland		Guinea
Taiwan	The United Arab Emirates	Italy		Guinea-Bissau
Tajikistan	Yemen	Kosovo		Kenya
Thailand		Latvia		Lesotho
Turkmenistan		Liechtenstein		Liberia
Uzbekistan		Lithuania		Madagascar
Vietnam		Luxembourg		Malawi
		Macedonia		Mali
		Malta		Mauritania
		Moldova		Mauritius
		Monaco		Mozambique
		Montenegro		Namibia
		Netherlands		Niger
		Norway		Nigeria
		Poland		Rwanda
		Portugal		Sao Tome and Principe
		Romania		Senegal
		Russia		Seychelles
		San Marino		Sierra Leone
		Serbia		South Africa
		Slovakia		South Sudan
		Slovenia		Sudan
		Spain		Swaziland
		Sweden		Tanzania
		Switzerland		Togo
		Ukraine		Uganda
		United Kingdom of Great Britain and Northern Ireland		Zambia
		Vatican City		Zimbabwe

Supplementary information Table S2.3. Papers used for this systematic literature review on pythons.

Authors	Title	Year
Savage, T.S.	Observations on the habits of the <i>Python natalensis</i>	1844
Hatch, J.L.	Some original investigations upon <i>Python molurus</i>	1890
Frazzetta, T.H.	Studies on the Morphology and Function of the Skull in the Boidae (Serpentes).: Cranial Differences Between <i>Python sebae</i> and <i>Epicrates Cenchris</i>	1959
Frazzetta, T.H.	Studies on the morphology and function of the skull of the Boidae (Serpentes). Part II. Morphology and function of the jaw apparatus in <i>Python sebae</i> and <i>Python mozapub</i>	1966
Williamson, M.A.	Notes on the growth rate of <i>Python reticulatus</i> (Serpentes: Boidae)	1967
Webb, G., Heatwole, H.	Patterns of Heat Distribution withing the Bodies of some Australian Pythons	1971
Logan, T.	A note on attempted breeding in captive <i>Python anchietae</i>	1973
Logan, T.	Observations on the bail python (<i>Python regius</i>) in captivity at Houston Zoological Gardens	1973
Sharma, B.D.	The variation in the distribution of the Indian python (<i>Python molurus molurus</i>)(Serpentes: Boidae) in Jammu Province	1973
Vinegar, A.	The effects of temperature on the growth and development of embryos of the Indian python, <i>Python molurus</i> (Reptilia: Serpentes: Boidae)	1973
Greene, H.	Defensive tail display by snakes and amphisbaenians	1973
Branch B., Patterson P.	Notes on the development of embryos of the African rock python, <i>Python sebae</i> (Serpentes: Boidae)	1974
Johnson, C.R., Webb, G.J.W., Johnson, C.	Thermoregulation in pythons: III. Thermal ecology and behavior of the black-headed rock python, <i>Aspidites melanocephalus</i>	1975
Van Mierop, L.H.S., Barnard, S.M.	Thermoregulation in a brooding female <i>Python molurus bivittatus</i> (Serpentes: Boidae)	1976
Van Mierop, L.H.S., Barnard, S.M.	Observations on the reproduction of <i>Python molurus bivittatus</i> (Reptilia, Serpentes, Boidae)	1976
Murphy, J.B., Carpenter, C.C., Gillingham, J.C.	Caudal luring in the green tree python, <i>Chondropython viridis</i> (Reptilia, Serpentes, Boidae)	1978
Van Mierop, L.H.S., Barnard, S.M.	Further observations on thermoregulation in the brooding female <i>Python molurus bivittatus</i> (Serpentes: Boidae)	1978

Panzica Viglietti, C., Panzica G.C.	Extrafusal motor endings in <i>Python reticulatus</i> (Schneider) costocutaneoinferiores muscles (Serpentes, Boidae)	1978
Barker, D.G., Murphy, J.B., Smith, K.W.	Social behavior in a captive group of Indian pythons, <i>Python molurus</i> (Serpentes, Boidae) with formation of a linear social hierarchy	1979
Platt, T.R., Bush, A.O.	<i>Spinicauda regiensis</i> n. Sp.(Nematoda: Heterakoidea), a parasite of the ball python (<i>Python regius</i>)	1979
Acharjyo, L.N., Misra, Ch. G.	Growth rate of Indian python <i>Python molurus molurus</i> (Serpentes: Boidae) in captivity with special reference to age at first egg-laying	1980
Branch, W.R., Hacke, W.D.,	A fatal attack on a young boy by an African rock python <i>Python sebae</i>	1980
Smith, L.A.,	A revision of the <i>Liasis olivaceus</i> species-group (Serpentes: Boidae) in Western Australia	1981
Smith, L.A.,	A revision of the python genera <i>Aspidites</i> and <i>Python</i> (Serpentes: Boidae) in Western Australia	1981
Gillingham, J.C., Chambers, J. A.,	Courtship and pelvic spur use in the Burmese python, <i>Python molurus bivittatus</i>	1982
Marcellini, D.L., Peters, A.,	Preliminary observations on Endogeneous heat production after feeding in <i>Python molurus</i>	1982
in den Bosch, H.A.J.,	Snout temperatures of reptiles, with special reference to the changes during feeding behaviour in <i>Python molurus bivittatus</i> (Serpentes, Boidae): a study using infrared radiation	1983
Ten Donkelaar, H.J., Bangma, G.C., De Boer-Van Huizen, R.,	Reticulospinal and vestibulospinal pathways in the snake <i>Python regius</i>	1983
Ten Donkelaar, H.J., Bangma, G.C.,	A crossed rubrobulbar projection in the snakepython <i>regius</i>	1983
Branch, B., Erasmus, H.,	Captive breeding of pythons in South Africa, including details of an interspecific hybrid (<i>Python sebae natalensis</i> x <i>Python molurus bivittatus</i>)	1984
Banks, C., Schwaner, T.D.,	Two cases of interspecific hybridization among captive Australian boid snakes	1984
Kroese F.G.M., Leceta J., Döpp E.A., Herraes M.P., Nieuwenhuis P., Zapata A.	Dendritic immune complex trapping cells in the spleen of the snake, <i>Python reticulatus</i>	1985
Ahne, W., Thomsen, I., Winton, J.,	Isolation of a reovirus from the snake, <i>Python regius</i>	1987
Ellis, T.M., Chappell, M.A.,	Metabolism, temperature relations, maternal behavior, and reproductive energetics in the ball python (<i>Python regius</i>)	1987
Slip D.J., Shine R.	Thermophilic response to feeding of the diamond python, <i>Morelia s. spilota</i> (Serpentes: Boidae)	1988
Smeets, W.J.A.J.,	Distribution of dopamine immunoreactivity in the forebrain and midbrain of the snake <i>Python regius</i> : a study with antibodies against dopamine	1988

Morgan D.R.	The use of oxytocin to relieve dystocia in a royal python (<i>Python regius</i>) (Serpentes: Boidae)	1988
Hammond, D.L., Dorsett, W.A.,	Tick infestation in a ball python (<i>Python regius</i>).	1988
Slip D.J., Shine R.	Habitat use, movements and activity patterns of free-ranging diamond pythons, <i>Morelia spilota spilota</i> (Serpentes: Boidae): A radiotelemetric study	1988
Slip, D.J., Shine, R.	Feeding habits of the diamond python, <i>Morelia s. spilota</i> : ambush predation by a boid snake	1988
Slip D.J., Shine R.	The reproductive biology and mating system of diamond pythons, <i>Morelia spilota</i> (Serpentes: Boidae)	1988
Morgan, D.R., Boycott, R.C.	A Report on the Angola Dwarf Python (<i>Python anchietae</i>) at Transvaal Snake Park	1990
Shine R., Slip D.J.	Biological aspects of the adaptive radiation of Australasian pythons (Serpentes: Boidae)	1990
Smeets W.J.A.J., Sevensma J.J., Jonker A.J.	Comparative analysis of vasotocin-like immunoreactivity in the brain of the turtle <i>Pseudemys scripta elegans</i> and the snake <i>Python regius</i>	1990
Underwood G., Stimson A.F.	A classification of pythons (Serpentes: Pythoninae)	1990
Hilf, M., Swanson, D., Wagner, R., Yu, V.L.	Pharmacokinetics of piperacillin in blood pythons (<i>Python curtus</i>) and in vitro evaluation of efficacy against aerobic gram-negative bacteria	1991
Hilf M., Swanson D., Wagner R., Yu V.L.	A new dosing schedule for gentamicin in blood pythons (<i>Python curtus</i>): a pharmacokinetic study	1991
Cooper Jr, W.E.	Discrimination of integumentary prey chemicals and strike-induced chemosensory searching in the ball python, <i>Python regius</i>	1991
Kuchling, G.	Seasonal variations of spermatogenesis and of the sexual segment of the kidney in the Carpet Python, <i>Morelia spilota</i> (Serpentes: Boidae)	1991
Williams, D.	“Natural” incubation by a Children's python, <i>Liasis maculosus</i> (Peters, 1873)(Serpentes: Boidae), under public display conditions	1992
Klingenberg, R.J.	A comparison of fenbendazole and ivermectin for the treatment of nematode parasites in ball pythons, <i>Python regius</i>	1992
Ogawa, M., Ahne, W., Essbauer, S.	Reptilian viruses: adenovirus-like agent isolated from Royal python (<i>Python regius</i>)	1992
Kobayashi, S., Kishida, R., Goris, R.C., Yoshimoto, M., Ito, H.	Visual and infrared input to the same dendrite in the tectum opticum of the python, <i>Python regius</i> : electron-microscopic evidence	1992
Kreger, M.D., Mench, J.A.	Physiological and behavioral effects of handling and restraint in the ball python (<i>Python regius</i>) and the blue-tongued skink (<i>Tiliqua scincoides</i>)	1993
Pearson, D.J.	Distribution, status and conservation of pythons in Western Australia	1993

Kluge, A.G.	Aspidites and the phylogeny of pythonine snakes	1993
Secor, S.M.	Digestive response to the first meal in hatchling Burmese pythons (<i>Python molurus</i>)	1995
Kobayashi, S., Amemiya, F., Kishida, R., Goris, R.C., Kusunoki, T., Ito, H.	Somatosensory and visual correlation in the optic tectum of a python, <i>Python regius</i> : a horseradish peroxidase and Golgi study	1995
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Ellis, R.J.	Corrections of the type specimens of <i>Liasis olivaceus barroni</i> Smith, 1981 (Serpentes: Pythonidae)	2015
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Kaye, S.W., Daverio, H., Eddy, R., Ossiboff, R.J., Peters-Kennedy, J., Morrissey, J.K.	Surgical resection of an interrenal cell adenocarcinoma in a woma python (<i>Aspidites ramsayi</i>) with 18 month follow-up	2016
Schilliger, L., Chetboul, V., Damoiseaux, C., Nicolier, A.	Restrictive cardiomyopathy and secondary congestive heart failure in a McDowell's carpet python (<i>Morelia spilota mcdowelli</i>)	2016
Penning, D.A., Dartez, S.F.	Size, but not experience, affects the ontogeny of constriction performance in ball pythons (<i>Python regius</i>)	2016

Mallery C.S., Jr., Carrillo M.M.	A case study of sex-linkage in <i>Python regius</i> (Serpentes: Boidae), with new insights into sex determination in Henophidia	2016
Sonibare, A.O., Ajuwape, A.T.P., Egbetade, A.O., Adediran, O.A., Adejinmi, J.O., Adedokun, R.A.M.	Dysecdysis secondary to anaphylactic reaction in a captive royal python (<i>Python regius</i>) at the Zoological Garden, Ibadan, Nigeria	2016
Sadler, R.A., Schumacher, J.P., Rathore, K., Newkirk, K.M., Cole, G., Seibert, R., Cekanova, M.	Evaluation of the role of the cyclooxygenase signaling pathway during inflammation in skin and muscle tissues of ball pythons (<i>Python regius</i>)	2016
Nørgaard, S., Andreassen, K., Malte, C.L., Enok, S., Wang, T.	Low cost of gastric acid secretion during digestion in ball pythons	2016
Enok, S., Leite, G.S.P.C., Leite, C.A.C., Gesser, H., Hedrick, M.S., Wang, T.	Improved cardiac filling facilitates the postprandial elevation of stroke volume in <i>Python regius</i>	2016
Darrow, B.G., Myers, G.E., KuKanich, B., Sladky, K.K.	Fentanyl transdermal therapeutic system provides rapid systemic fentanyl absorption in two ball pythons (<i>Python regius</i>)	2016
Nielsen, E.L., Hespel, A., Kottwitz, J.J., Cole, R.	Evaluation of the follicular cycle in ball pythons (<i>Python regius</i>)	2016
Williams, C.J.A., James, L.E., Bertelsen, M.F., Wang, T.	Tachycardia in response to remote capsaicin injection as a model for nociception in the ball python (<i>Python regius</i>)	2016
Habroun, S.	Effects of Food Consumption on Neurogenesis in juvenile <i>Python regius</i>	2016
Galecki, R., Sokol, R., Dudek, A.	Tongue worm (<i>Pentastomida</i>) infection in ball pythons (<i>Python regius</i>)-a case report	2016
Bertocchi, M., Pelizzone, I., Parmigiani, E., Beltrami, F., Manfredi, S., Di Ianni, F.	Observations of the female reproductive cycle of captive royal pythons (<i>Python regius</i>) using ultrasound imaging	2016
Bertocchi, M., Di Ianni, F., Bresciani, C., Volta, A., Bigliardi, E., de Cesaris, V., Ponzio, P., Macchi, E., Parmigiani, E.	Ultrasound monitoring of female reproductive cycle in captive royal pythons (<i>Python regius</i>): preliminary observations.	2016
Boback, S.M., Snow, R.W., Hsu, T., Peurach, S.C., Dove, C.J., Reed, R.N.	Supersize me: remains of three white-tailed deer (<i>Odocoileus virginianus</i>) in an invasive Burmese python (<i>Python molorus bivittatus</i>) in Florida.	2016
Walters, T.M., Mazzotti, F.J., Fitz, H.C.	Habitat selection by the invasive species Burmese python in southern Florida	2016
Mazzotti, F.J., Rochford, M., Vinci, J., Jeffery, B.M., Eckles, J.K., Dove, C., Sommers, K.P.	Implications of the 2013 Python Challenge® for ecology and management of <i>Python molorus bivittatus</i> (Burmese Python) in Florida	2016
Wolf, A.J., Walters, T.M., Rochford, M.R., Snow, R.W., Mazzotti, F.J.	Incubation temperature and sex ratio of a <i>Python bivittatus</i> (Burmese python) clutch hatched in Everglades National Park, Florida	2016
Hanifa, B.F., Nugraha, A.P., Nanda, I.F., Daryono, B.S.	Phylogenetic analysis of <i>Malayopython reticulatus</i> (Schneider, 1801) from southern Sulawesi based on morphological and molecular character	2016
Natusch, D.J.D., Lyons, J.A., Mumpuni, R.A., Shine, R.	Jungle giants: assessing sustainable harvesting in a difficult-to-survey species (<i>Python reticulatus</i>)	2016
Corey B., Doody J.S.	Black box and attics: Habitat selection and resource use by large threatened pythons in landscapes with contrasting human modification	2016

Lobo J.V., Sreepada K.S.	First report of leucism in <i>Python molurus molurus</i> (Serpentes: Pythonidae) from Mangalore, Karnataka, India	2016
Esquerré D., Scott KJ.	Parallel selective pressures drive convergent diversification of phenotypes in pythons and boas	2016
Brusch, G.A., Billy, G., Blattman, J.N., DeNardo, D.F.	Reproduction alters hydration state but does not impact the positive effects of dehydration on innate immune function in Children's pythons (<i>Antaresia childreni</i>)	2017
Dervas, E., Hepojoki, J., Laimbacher, A., Romero-Palomo, F., Jelinek, C., Keller, S., Smura, T., Hepojoki, S., Kipar, A., Hetzel, U.	Nidovirus-associated proliferative pneumonia in the green tree python (<i>Morelia viridis</i>)	2017
Ducrotte-Tassel, A., Kirilov, P., Salvi, J., Czyz, I., Doré, V., Marignac, G., Pignon, C., Boulieu, R., Perrot, S.	Detection of enrofloxacin after single-dose percutaneous administration in <i>Python regius</i> , <i>Boa constrictor imperator</i> , and <i>Acrantophis dumerili</i>	2017
Bertocchi, M., Pelizzone, I., Parmigiani, E., Ponzio, P., Macchi, E., Bigliardi, E., Bresciani, C., Denti, L., Di Ianni, F.	Progesterone role in the regulation of the female reproductive cycle in captive royal python (<i>P. Regius</i>): preliminary study	2017
Jakobsen, S.L., Williams, C.J.A., Wang, T., Bertelsen, M.F.	The influence of mechanical ventilation on physiological parameters in ball pythons (<i>Python regius</i>)	2017
Ryerson, W.G., Tan, W.	Strike kinematics and performance in juvenile ball pythons (<i>Python regius</i>)	2017
Habroun, S.S.	Effects of food consumption on cell proliferation in the brain of <i>Python regius</i>	2017
Gamble, T., Castoe, T.A., Nielsen, S.V., Banks, J.L., Card, D.C., Schield, D.R., Schuett, G.W., Booth, W.	The discovery of XY sex chromosomes in a boa and python	2017
Willson J.D.	Indirect effects of invasive Burmese pythons on ecosystems in southern Florida	2017
Murray-Dickson, G., Ghazali, M., Ogden, R., Brown, R., Auliya, M.	Phylogeography of the reticulated python (<i>Malayopython reticulatus</i> ssp.): Conservation implications for the worlds' most traded snake species	2017
Bhattarai S., Pokheral C.P., Lamichhane B.R.	Death feigning behavior in the Burmese python <i>Python bivittatus</i> Kuhl, 1820 in Chitwan National Park, Nepal	2017
Duan, Y., Wang, Y., Bai, S., Tian, X., Rong, K., Ma, J.	Genetic diversity and population genetic structure of <i>Python bivittatus</i> in China	2017
Natusch D.J.D., Carter J.F., Aust P.W., Van Tri N., Tinggi U., Mumpuni, Riyanto A., Lyons J.A.	Serpent's source: Determining the source and geographic origin of traded python skins using isotopic and elemental markers	2017
Esquerré D., Sherratt E., Keogh J.S.	Evolution of extreme ontogenetic allometric diversity and heterochrony in pythons, a clade of giant and dwarf snakes	2017
Singh, J., Mallik, S., Nath, I., Acharya, A., Das, S.P., Sethi, S., Sahoo, M.	Infectious stomatitis in an Indian rock python (<i>Python molurus</i>) and its therapeutic management	2018
Krishnasamy, V.	Notes from the field: investigation of an outbreak of Salmonella Paratyphi B variant L (+) tartrate+(Java) associated with ball python exposure—United States, 2017	2018

Bunke, L.G., Sladky, K.K., Johnson, S.M.	Antinociceptive efficacy and respiratory effects of dexmedetomidine in ball pythons (<i>Python regius</i>)	2018
Yaw, T.J., Mans, C., Johnson, S.M., Doss, G.A., Sladky, K.K.	Effect of injection site on alfaxalone-induced sedation in ball pythons (<i>Python regius</i>)	2018
Bertocchi, M., Pelizzone, I., Parmigiani, E., Ponzio, P., Macchi, E., Righi, F., Di Girolamo, N., Bigliardi, E., Denti, L., Bresciani, C.	Monitoring the reproductive activity in captive bred female ball pythons (<i>P. Regius</i>) by ultrasound evaluation and noninvasive analysis of faecal reproductive hormone (progesterone and 17 β -estradiol) metabolites trends	2018
Miller, L.J., Fetterer, D.P., Garza, N.L., Lackemeyer, M.G., Donnelly, G.C., Steffens, J.T., Van Tongeren, S.A., Fiallos, J.O., Moore, J.L., Marko, S.T.	A fixed moderate-dose combination of tiletamine+ zolazepam outperforms midazolam in induction of short-term immobilization of ball pythons (<i>Python regius</i>)	2018
James, L.E., Williams, C.J.A., Bertelsen, M.F., Wang, T.	Anaesthetic induction with alfaxalone in the ball python (<i>Python regius</i>): dose response and effect of injection site	2018
Hoon-Hanks, L.L., Layton, M.L., Ossiboff, R.J., Parker, J.S.L., Dubovi, E.J., Stenglein, M.D.	Respiratory disease in ball pythons (<i>Python regius</i>) experimentally infected with ball python nidovirus	2018
Hunter, M.E., Johnson, N.A., Smith, B.J., Davis, M.C., Butterfield, J.S.S., Snow, R.W., Hart, K.M.	Cytoskeletal discordance in the Florida Everglades invasive Burmese python (<i>Python bivittatus</i>) population reveals possible hybridization with the Indian python (<i>P. Molurus</i>)	2018
Bartoszek, I.A., Andreadis, P.T., Prokopervin, C., Curry, G., Reed, R.N.	<i>Python bivittatus</i> (burmese python) and <i>Gopherus polyphemus</i> (gopher tortoise).	2018
Mutascio, H.E., Pittman, S.E., Zollner, P.A., D'Acunto, L.E.	Modeling relative habitat suitability of southern Florida for invasive Burmese pythons (<i>Python molurus bivittatus</i>)	2018
Reeves, L.E., Krysko, K.L., Avery, M.L., Gillett-Kaufman, J.L., Kawahara, A.Y., Connelly, C.R., Kaufman, P.E.	Interactions between the invasive Burmese python, <i>Python bivittatus</i> Kuhl, and the local mosquito community in Florida, USA	2018
Maulidi, A., Fatchiyah, F., Hamidy, A., Kurniawan, N.	Microsatellite marker for cross-species amplification: Study case for Indonesian Sundaland python (Serpentes: Pythonidae)	2018
Fitzgerald, M., Shine, R.	Mate-guarding in free-ranging carpet pythons (<i>Morelia spilota</i>)	2018
Sianturi, M.M.P., Jumilawaty, E., Hartanto, A.	Predicting size limit of wild blood python (<i>Python brongersmai</i> stull, 1938) harvesting in north Sumatera	2018
Matojo, N.D.	Head dimorphism in the African python, <i>Python natalensis</i> (Squamata: Pythonidae) from Tanzania	2018
Alexander G.J.	Reproductive biology and maternal care of neonates in southern African python (<i>Python natalensis</i>)	2018
Ciavaglia, S., Linacre, A.	Ozpythonplex: An optimised forensic STR multiplex assay set for the Australasian carpet python (<i>Morelia spilota</i>)	2018
Hoser, R., Home, I.C.Z.N.	Coming back up! The first ever documented cases of fur ball regurgitation by a black-headed python (Serpentes: Pythonidae: Aspidites).	2019

Paillusseau, C., Gandar, F., Schilliger, L., Lavennes, M., Poissonnier, C., Damoiseaux, C., Nicolier, A., Chetboul, V.	Atrioventricular stenosis and insufficiency associated with chronic endocarditis in a jungle carpet python (<i>Morelia spilota cheynei</i>)	2019
Larouche, C.B., Johnson, R., Beaudry, F., Mosley, C., Gu, Y., Zaman, K.A., Beaufrère, H., Dutton, C.	Pharmacokinetics of midazolam and its major metabolite 1-hydroxymidazolam in the ball python (<i>Python regius</i>) after intracardiac and intramuscular administrations	2019
Larouche, C.B., Beaufrère, H., Mosley, C., Nemeth, N.M., Dutton, C.	Evaluation of the effects of midazolam and flumazenil in the ball python (<i>Python regius</i>)	2019
Busse, H., Huptas, C., Baumgardt, S., Loncaric, I., Spargser, J., Scherer, S., Wenning, M., Kämpfer, P.	Proposal of <i>Lysobacter pythonis</i> sp. Nov. Isolated from royal pythons (<i>Python regius</i>)	2019
Larouche, C.B., Mosley, C., Beaufrère, H., Dutton, C.	Effects of midazolam and nitrous oxide on the minimum anesthetic concentration of isoflurane in the ball python (<i>Python regius</i>)	2019
Larouche, C.B.	The use of midazolam, isoflurane, and nitrous oxide for sedation and anesthesia of ball pythons (<i>Python regius</i>)	2019
Orzechowski, S.C.M., Romagosa, C.M., Frederick, P.C.	Invasive Burmese pythons (<i>Python bivittatus</i>) are novel nest predators in wading bird colonies of the Florida Everglades	2019
Rumbold, D.G., Bartoszek, I.A.	Mercury concentrations in invasive Burmese pythons (<i>Python bivittatus</i>) of Southwest Florida	2019
Hunter M.E., Meigs-Friend G., Ferrante J.A., Smith B.J., Hart K.M.	Efficacy of eDNA as an early detection indicator for Burmese pythons in the ARM Loxahatchee National Wildlife Refuge in the greater Everglades ecosystem	2019
Swan, G., Harvey, C.	An observation of excavating behaviour by a black-headed python (<i>'Aspidites melanocephalus'</i>) in the wild	2019
Septiadi, L., Fathoni, M., Hanifa, B.F., Hamidy, A.	Morphological variation of <i>Malayopython reticulatus</i> Schneider, 1801) from several population in Indonesia	2019
Robbins, A., Loader, J., de Villiers, D., Beyer, H.L., Hanger, J.	Predation by carpet pythons (<i>Morelia spilota</i>) is an important cause of mortality in a free-living koala (<i>Phascolarctos cinereus</i>) population in South East Queensland	2019
Natusch D.J.D., Lyons J.A., Riyanto A., Mumpuni, Shine R.	Interspecific divergence in biological attributes of short-tailed pythons (<i>Python breitensteini</i> and <i>P. Brongersmai</i>) from Kalimantan and Sumatra	2019
Augstenová B., Mazzoleni S., Kostmann A., Altmanová M., Frynta D., Kratochvíl L., Rovatsos M.	Cytogenetic analysis did not reveal differentiated sex chromosomes in ten species of boas and pythons (Reptilia: Serpentes)	2019
Natusch, D.J.D., Lyons, J.A., Riyanto, A., Khadiejah, S.	Applying skin-size limits for management of trade in Asian reptile skins	2020
da Silva Vasconcelos, E., Kalinin, A.L., Cipriano, R.C., dos Santos Beserra, S., Lopes, A.G., da Costa Leite, C.A., Monteiro, D.A.	Effects of feeding and digestion on myocardial contractility and expression of calcium-handling proteins in Burmese pythons (<i>Python molurus</i>)	2020
Ahmed, M.F.E., Alssahen, M., Lämmler, C., Eisenberg, T., Plötz, M., Abdulmawjood, A.	Studies on Trueperella pyogenes isolated from an okapi (<i>Okapia johnstoni</i>) and a royal python (<i>Python regius</i>)	2020
Li, W., Lee, M., Tseng, Y., Yang, N.	A case report of reptile-associated nidovirus (serpentovirus) in a ball python (<i>Python regius</i>) in Taiwan	2020

Michaely, L.M., von Dörnberg, K., Molnár, V., Tappe, D., Tannich, E., Hewicker-Trautwein, M., Wohlsein, P.	Entamoeba ranarum infection in a ball python (<i>Python regius</i>)	2020
D'Cruze, N., Bates, J., Assou, D., Ronfot, D., Coulthard, E., Segniagbeto, G.H., Auliya, M., Megson, D., Rowntree, J.	A preliminary assessment of bacteria in “ranché” ball pythons (<i>Python regius</i>), Togo, West Africa	2020
Garcia-Elfring, A., Roffey, H.L., Hendry, A.P., Barrett, R.D.H.	A nonsense mutation in TFEC is the likely cause of the recessive piebald phenotype in ball pythons (<i>Python regius</i>)	2020
Jensen, M.F., Nedergaard, S., Nielsen, H.N., Skovgaard, N., Stevnsner, T.V., Wang, T.	Endothelin-1 induces a strong pressor effect in ball pythons (<i>Python regius</i>)	2020
Amemiya, F., Goris, R.C., Atobe, Y., Ishii, N., Kusunoki, T.	The ultrastructure of infrared receptors in a boid snake, <i>Python regius</i> : evidence for periodic regeneration of the terminals	2020
Pigoli, C., Gambini, M., Bardi, E., Bassi, J., Manfredi, M., Ghisleni, G., Tecilla, M.	Congenital skull malformation in a captive python (<i>Pythus regius</i>)	2020
Yaw, T.J., Mans, C., Johnson, S., Bunke, L., Doss, G.A., Sladky, K.K.	Evaluation of subcutaneous administration of alfaxalone-midazolam and dexmedetomidine-midazolam for sedation of ball pythons (<i>Python regius</i>)	2020
Paillusseau, C., Gandar, F., Schilliger, L., Chetboul, V.	Two-dimensional echocardiographic measurements in the ball python (<i>Python regius</i>)	2020
Ryerson, W.G.	Ontogeny of strike performance in ball pythons (<i>Python regius</i>): a three-year longitudinal study	2020
Fox, B.C., Hogan, S.	Hypopigmentation as the cause for the neurological disorder “Spider Wobble” in <i>Python regius</i>	2020
Kawase, K., Yoshida, S., Nakagun, S., Kobayashi, Y., Shiihara, S.	Disseminated infection disease with three nontuberculous mycobacteria in a ball python (<i>Python regius</i>).	2020
Martinez, M.	Growth and feeding response in <i>Python regius</i> in ambient temperature vs. hot-spot	2020
D'Cruze, N., Harrington, L.A., Assou, D., Green, J., Macdonald, D.W., Ronfot, D., Segniagbeto, G.H., Auliya, M.	Betting the farm: A review of ball python and other reptile trade from Togo, West Africa	2020
Cacioppo, J.A., Perry, S.M., Rockwell, K., Mitchell, M.A.	A survey of husbandry and breeding techniques in the ball python (<i>Python regius</i>) pet trade	2020
Nafus, M.G., Mazzotti, F.J., Reed, R.N.	Estimating detection probability for Burmese pythons with few detections and zero recaptures	2020
Saunders, D.A., Mawson, P.R., Dawson, R.	Predation by southwestern carpet python (<i>Morelia spilota imbricata</i>) of Carnaby's cockatoo (<i>Calyptorhynchus latirostris</i>) in a breeding hollow	2020
Natusch, D.J.D., Esquerré, D., Lyons, J.A., Hamidy, A., Lemmon, A.R., Lemmon, E.M., Riyanto, A., Keogh, J.S., Donnellan, S.	Species delimitation and systematics of the green pythons (<i>Morelia viridis</i> complex) of Melanesia and Australia	2020

Shafi, S., Maurya, K.K., Ojha, G., Mall, A., Roy, H.	Sightings of Burmese pythons (<i>Python bivittatus</i>) in and around the Valmiki Tiger Reserve, Bihar, India	2020
Natusch D.J.D., Lyons J.A., Mumpuni, Riyanto A., Shine R.	Harvest effects on blood pythons in North Sumatra	2020
Auliya, M., Hofmann, S., Segniagbeto, G.H., Assou, D., Ronfot, D., Astrin, J.J., Forat, S., Ketoh, G.K.K., D'Cruze, N.	The first genetic assessment of wild and farmed ball pythons (Reptilia, Serpentes, Pythonidae) in southern Togo	2020
D'Cruze, N., Harrington, L.A., Assou, D., Ronfot, D., Macdonald, D.W., Segniagbeto, G.H., Auliya, M.	Searching for snakes: Ball python hunting in southern Togo, West Africa.	2020
Harrington, L.A., Green, J., Muinde, P., Macdonald, D.W., Auliya, M., D'Cruze, N.	Snakes and ladders: A review of ball python production in West Africa for the global pet market	2020
Georgalis G.L., Mayda S., Alpagut B., Şarbak A., Güler G.	The Westernmost Asian record of pythonids (Serpentes): The presence of python in a Miocene Hominoid locality of Anatolia	2020
Rungnirundorn, T., Khamchomphu, N., Senarat, N., Duangurai, T.	Alternative treatment of stomatitis in ball python (<i>Python regius</i>) with class IV laser therapy	2021
Karklus, A.A., Sladky, K.K., Johnson, S.M.	Respiratory and antinociceptive effects of dexmedetomidine and doxapram in ball pythons (<i>Python regius</i>)	2021
Tamai, I.A., Pakbin, B., Kafı, Z.Z., Brück, W.M.	Oral abscess caused by <i>Chryseobacterium indologenes</i> in ball python (<i>Python regius</i>), A case report	2021
Hansen, L.M.B., Wang, T.	The vasopressor action of angiotensin II (ANG II) in ball pythons (<i>Python regius</i>)	2021
Tillis, S.B., Iredale, M.E., Childress, A.L., Graham, E.A., Wellehan, J.F.X., Isaza, R., Ossiboff, R.J.	Oral, cloacal, and hemipenial actinomycosis in captive ball pythons (<i>Python regius</i>)	2021
Boukens, B.J.D., Joyce, W., Kristensen, D.L., Hooijkaas, I., Jongejan, A., Wang, T., Jensen, B.	Catecholamines are key modulators of ventricular repolarization patterns in the ball python (<i>Python regius</i>)	2021
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Kwon, J., Kim, S.W., Kim, Sang G., Kim, H.J., Lee, S.B., Kang, J.W., Jung, W.J., Giri, S.S., Lee, K., Park, S. C.	A Case of submandibular leiomyosarcoma, mimicking an abscess, in a ball python (<i>Python regius</i>)	2021
Hetzel, U., Korzyukov, Y., Keller, S., Szivovica, L., Pesch, T., Vapalahti, O., Kipar, A., Hepojoki, J.	Experimental reptarenavirus infection of <i>Boa constrictor</i> and <i>Python regius</i>	2021
Toro, A., Abdel-Aal, H.A., Zuluaga, E., Cuervo, P., Ballesteros, L.M., Sánchez, J.C., Rudas, J.S., Isaza, C., Misiolek, W.Z.	Influence of surface morphology and internal structure on the mechanical properties and tribological response of Boa red tail and <i>Python Regius</i> snake skin	2021
Ledbetter, E.C., Marion, J.S., Morrissey, J.K.	Amniotic membrane grafting for traumatic complete spectaculoectomy and keratomalacia in a Boelen's python (<i>Simalia boeleni</i>)	2021

Whitney, N.M., White, C.F., Smith, B.J., Cherkiss, M.S., Mazzotti, F.J., Hart, K.M.	Accelerometry to study fine-scale activity of invasive Burmese pythons (<i>Python bivittatus</i>) in the wild	2021
Josimovich, J.M., Falk, B.G., Grajal-Puche, A., Hanslowe, E.B., Bartoszek, I.A., Reed, R.N., Currylow, A.F.	Clutch may predict growth of hatchling Burmese pythons better than food availability or sex	2021
Pittman, S.E., Bartoszek, I.A.	Initial dispersal behavior and survival of non-native juvenile Burmese pythons (<i>Python bivittatus</i>) in South Florida	2021
Bartoszek, I.A., Smith, B.J., Reed, R.N., Hart, K.M.	Spatial ecology of invasive Burmese pythons in southwestern Florida	2021
Esquerré, D., Donnellan, S.C., Pavón-Vázquez, C.J., Fenker, J., Keogh, J.S.	Phylogeography, historical demography and systematics of the world's smallest pythons (Pythonidae, Antaresia)	2021
Natusch, D.J.D., Esquerré, D., Lyons, J.A., Hamidy, A., Lemmon, A.R., Lemmon, E.M., Riyanto, A., Keogh, J.S., Donnellan, S.	Phylogenomics, biogeography and taxonomic revision of New Guinean pythons (Pythonidae, Leiopython) harvested for international trade	2021
Natusch, D.J.D., Lyons, J.A.	Geographic frequency and ecological correlates of juvenile colour polymorphism in green pythons (<i>Morelia azurea</i> and <i>Morelia viridis</i>)	2021
Kufnerova, J.	A novel approach of using shed skins of the green tree python, <i>Morelia viridis</i> , for forensic purposes	2021
Vishnu, S.N., Ramesh, C., Thirumurugan, V., Sathish, C.	Size matters: First record of minimum male size at maturity and mating of free-ranging, endangered Indian python, <i>Python molurus</i> .	2021
Natusch D., Lyons J., Mears L.-A., Shine R.	Biting off more than you can chew: Attempted predation on a human by a giant snake (<i>Simalia amethystina</i>)	2021
Natusch D.J.D., Lyons J.A., Shine R.	Rainforest pythons flexibly adjust foraging ecology to exploit seasonal concentrations of prey	2021
Gaina, C.D., Niron, A.J.D., Foeh, N.D.F.K., Tophianong, T.C.	Ultrasound features of pregnancy in water python (<i>Liasis mackloti</i> ssp) reveals maternal egg provisioning: a case report.	2022
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CHAPTER 3

Southern African python (*Python natalensis*) diet, using information gathered from social media and historical data

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Running header: Diet of *Python natalensis*

3.1 Abstract

African pythons are the largest and among the most charismatic species of snake on the continent. Surprisingly little is known about the details of their diets. This may be due to the difficulty of compiling a list of prey items for a generalist species. We used data collected from historical literature and citizen science platforms, in the form of social media, to compile a baseline list of species that the southern African python (*Python natalensis*) feeds on, including birds, mammals, reptiles and fish. Data collected from social media significantly increased the list of prey species compared with those only known from historical literature records. In addition, the data revealed a shift from avian prey to more mammalian species and an increase in human-animal conflict involving larger pythons. Hunting behaviours were observed and caudal luring documented for the first time in this species. Social media can be a useful data source that, when used correctly, can provide a rich source of raw data that can be usefully analysed and combined with other sources in order to answer questions, as well as enrich and validate prior knowledge about cryptic and difficult to research species.

Keywords: Citizen Science; prey species; snake; social media; Pythonidae

3.2 Introduction

Many humans worldwide are fascinated by nature, spending large amounts of time and money in wilderness areas (Schultz 2002; Hausmann et al. 2017, 2018). Any interesting phenomena that are observed are usually documented with photographs. In recent years, social media platforms, such as Facebook® and Instagram®, have provided an easy and popular way to share these sightings online (Stieglitz et al. 2018). This provides a valuable source of citizen science data that is easy to collect and usually provides an approximate locality, date and description (Maritz et al. 2021). At the very least, the researcher can usually gather certain baseline data, even when no information is provided (Stieglitz et al. 2018).

Research projects focusing on elusive species often prove extremely challenging because of the secretive nature of the study species, especially when resources are limited (Durso et al. 2011). For these reasons, records that are available on social media platforms can be useful and are becoming an acceptable and recognised source of data collection (Silva et al. 2024; Phakoago et al. 2024). Using such resources has positive implications for increasing the understanding of evolutionary and ecological processes characterised by discrete and difficult-to-detect transient events, and this is possible through the increase in observation coverage and depth (Maritz and Maritz 2020).

Trophic interactions between species help to maintain ecosystems (McCann 2007), but documenting them is often difficult, costly, and time-consuming. These interactions, defined as one organism consuming another, form the basis of understanding system characteristics and processes, such as energy flow, food web dynamics, population dynamics and the evolution of physiological, morphological and behavioural adaptations by predators and prey (Garvey and

Whiles 2017). Feeding is often the predominant way that predators influence faunal communities (Dorcas et al. 2012).

Some groups of species, such as non-herbivorous, terrestrial vertebrates, have characteristics that reduce the likelihood of detection of trophic interactions and, as such, are underrepresented in literature (Miranda et al. 2013). In situations where these datasets exist, ectotherms tend to be less well represented than endotherms, primarily because endothermy demands a higher rate of food intake and thus an increase in ease of sampling (Miranda et al. 2013; Maritz and Maritz 2020). This is especially true of herpetofauna (Durso and Seigel 2015) because of their cryptic natural histories (Steen 2010) and infrequent and discrete feeding habits (Greene 1997; Shine and Bonnet 2000). Maritz et al. (2021) described a limited global knowledge of descriptive dietary studies on snakes and expressed the need for more research.

The southern African python (*Python natalensis*) is the largest snake in southern Africa, reaching a mass of 60 kg and a length of 6 m (Alexander and Marais 2007; Marais and Kemp 2022; Supplementary Figure S2.1). They occur from northern and eastern South Africa northwards to the equator (Alexander 2018; Tolley et al. 2023). Their diet is recorded as being varied, including mammals, reptiles, birds, birds' eggs and fish (Alexander 2012; Marais and Kemp 2022; Barends and Naik 2023). Pythons are reported to be primarily ambush predators, and feed irregularly when prey is available (Broadley 1983; Secor and Ott 2007). They can take prey of variable sizes, from small birds' eggs and rodents to large antelope and even humans (Branch and Haacke 1980; Broadley 1983; Alexander 2012).

Our study aimed to document the diet of the southern African python more comprehensively using historical, social media and observational data; to assess the use of social media for such studies; to establish how the python's diet changes according to age/size; and to

identify different hunting behaviours. We predicted an increased range of dietary items compared with historical data, that social media is a useful tool for obtaining dietary records, and that there would be an ontogenetic shift in diet as the pythons mature in size.

3.3 Methods

3.3.1 Historical data

During 2023 and early 2024, we gathered historical data on the southern African python diet from as many literature sources (including field guides, articles and short notes) as could be found. These included all those listed in the reptile database and a recent study by Barends and Naik (2023) that summarised some of the historic feeding records for the southern African python. We searched using Google Scholar®, Web of Science®, and Scopus® using the same terms as those used in the social media search, as outlined in the following section.

3.3.2 Social media

During 2023 and early 2024, we targeted specific Facebook® groups, Youtube® and Instagram® (Supplementary Table S3.1), which were likely to contain southern African python images for our data search. The data collected were those posted online until 01 May 2024. Firstly, we used the search word “python”, which was entered into the search bar on these groups. This resulted in all the posts containing this word being shortlisted and these were then manually processed. A similar process was followed for Instagram® and Youtube®; however, the search words “southern African python” and “*Python natalensis*” were used as these searches were not limited to South African posts. In addition, we conducted a specific search for southern African python on iNaturalist® and used only the ‘Research Grade’ posts. This method was not comprehensive as

posts where the snake was not identified did not get shortlisted. In all the posts that were used, it was possible to visually identify from the photographs that the snake in question was a southern African python, and the prey item was identified as precisely as possible.

We manually filtered each post, checking for relevance, with only justifiable information retrieved and the relevant data extracted. Snake sizes are frequently exaggerated, so all sightings were split into three categories: small (up to 1.5 m), medium (1.5 – 3 m) and large (larger than 3 m). We found it was feasible to roughly discern this scale from the photographs. The first author conducted this process so that the best estimate was standardised. In most cases (92.8%), it was possible to identify the prey to species level. When species-level identification was not possible, we identified the prey to the finest possible taxonomic level. The prey was identified using visible features from the photograph, for example, fur, feathers, limbs, etc. and the location to narrow down possible species. Additionally, in many instances, experts in wildlife identification had already confirmed the species of the prey item. We extracted the maximum amount of information from each record, including date, locality, species of prey item, size category of the snake, and any relevant notes.

3.3.3 Observations

Several of the southern African python feeding observations were personal observations made by the first author in the Kosi Bay Nature Reserve, KwaZulu-Natal province. Opportunistic targeted questioning of herpetology researchers and citizen scientists, for additional python dietary information, was also done to capture incidental feeding records that had not been recorded in the literature. These personal observations were from credible sources with extensive expertise in

wildlife observation and natural history, and who had spent extended periods in areas where pythons occurred.

3.3.4 Statistical analyses

We summarised the data found using descriptive statistics. We compared the historical and social media records. We analysed the frequency records of the social media data to establish the trends and range of the data. We conducted further statistical analyses using the Chi-squared test and the Shannon–Wiener diversity index (H' ; Magurran 1988) in R (R Core Team 2024).

3.4 Results

3.4.1 Geographical distribution of prey records

The contributions of southern African python prey records from southern and eastern Africa on social media were found to be significantly different ($\chi^2 = 917.67$, $df = 9$, $p < 0.001$), with the majority of the southern African python prey records from South Africa, 71.9% ($n = 151$). Zambia accounted for 8.0% with 17 records, and the remaining 26 records were distributed across Botswana ($n = 15$), Namibia ($n = 12$), Zimbabwe ($n = 5$), Malawi ($n = 4$), Mozambique ($n = 3$), and Kenya, Eswatini and Tanzania each having a single record (Figure 3.1). Of the records that came from South Africa, most came from Limpopo province ($n = 55$), followed by KwaZulu-Natal ($n = 41$), Mpumalanga ($n = 20$), North-West ($n = 6$), Gauteng ($n = 1$) and Eastern Cape ($n = 1$) provinces. Within South Africa, 22 of the 55 records for Limpopo came from within Kruger National Park, with several others coming from the surrounding lodges and reserves. We found that most of the social media records came from snake identification groups.

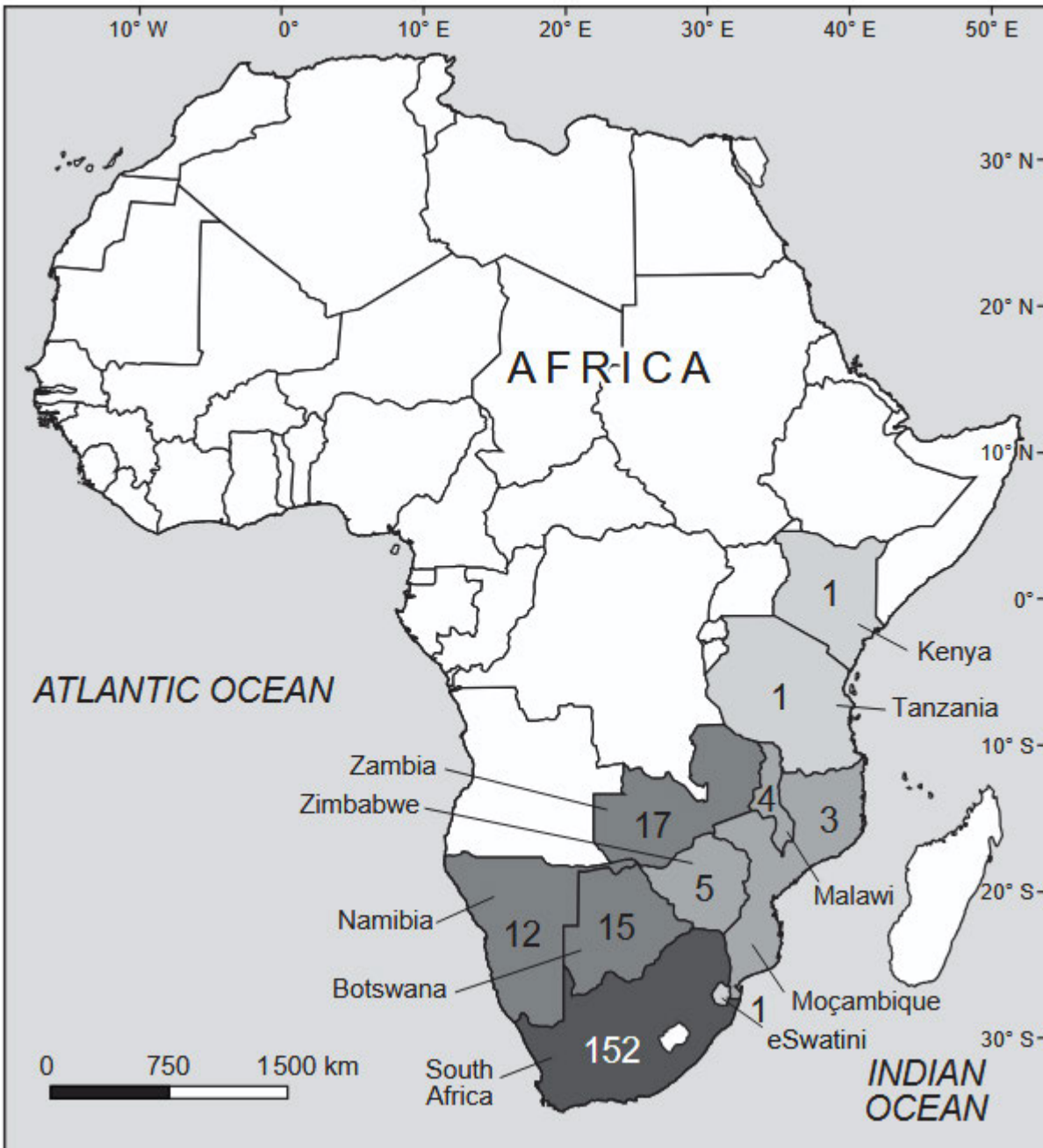


Figure 3.1: Map showing the distribution of the southern African python prey records per country in southern and eastern Africa.

3.4.2 Prey

The historical data we found on the southern African python diet documented records of 18 mammalian species, five avian species, three reptilian species and one species of fish (Table 3.1). The fish incidents were only recorded once, when two pythons were found drowned in small fish traps in Lake Sibaya, KwaZulu-Natal, South Africa. They were engorged and, when cut open, revealed cichlids, presumably taken from inside the traps (Bruton and Cooper 1980).

The data we retrieved from citizen science on social media of the southern African python diet resulted in 238 feeding observations, which included 36 mammalian species, 41 avian species, and two reptilian species (Table 3.2). Of the 238 records, 219 records (92.0%) could be identified to species level. Fifteen records (6.3%) were identified to family level. The remaining four records (1.7%) were only identified as either birds or fish (these were not included in Table 3.2 as they were not able to be identified to species level). We found significantly more feeding encounters involving mammalian prey than any other taxon ($\chi^2 = 242.88$, $df = 3$, $p < 0.001$).

The various social media platforms differed significantly in the number of southern African python prey records posted (Supplementary Table S3.1) ($\chi^2 = 440.97$, $df = 3$, $p < 0.001$). The majority (84.5%) of these social media records came from Facebook®, while Youtube® provided the second largest number of records (6.3%), and iNaturalist® and Instagram® contributed 5.0% and 4.2% respectively. Of these records, 58.0% ($n = 138$) were mammalian species, while 40.8% ($n = 97$) were avian species, and 1.3% ($n = 3$) were either reptilian or fish species.

The personal observations of southern African pythons feeding contributed a further 16 species to the list of known prey items (Table 3.3). These consisted of nine mammalian species and seven avian species (Table 3.3).

All of the sources combined resulted in a total list of 104 vertebrate species consumed by southern African pythons. The contributions from this study contributed significantly more than the historical data ($\chi^2 = 30.15$, $df = 1$, $p < 0.001$). Historical data accounted for 23.1% of the species, social media provided 61.5%, and observations contributed the remaining 15.4%.

Table 3.1: Prey species of southern African python from historical data sourced from the literature.

(Note: “A” indicates unsuccessful attempted feeding events of species, so not included in the number of prey species).

Common name	Latin name	References
Mammals		
Impala	<i>Aepyceros melampus</i>	(Branch and Haacke 1980)
Domestic dog	<i>Canis lupus familiaris</i>	(Broadley 1966)
Red duiker	<i>Cephalophus natalensis</i>	(Fitzsimons 1919)
Large spotted genet	<i>Genetta tigrina</i>	(Pernetta and Dell 2012)
Cape porcupine	<i>Hystrix africaeaustralis</i>	(Broadley 1983)
Waterbuck	<i>Kobus ellipsiprymnus</i>	(Broadley 1983)
Scub hare	<i>Lepus saxatilis</i>	(Dixon 1966)
Honey badger	<i>Mellivora capensis</i>	(Branch 1991)
Leopard	<i>Panthera pardus</i>	(Fitzsimons 1930)
Springhare	<i>Pedetes capensis</i>	(Broadley 1959)
Blue duiker	<i>Philantomba monticola</i>	(Fitzsimons 1930)
Rock hyrax	<i>Procavia capensis</i>	(Fitzsimons 1919; Broadley 1983)
Sharpe’s grysbok	<i>Raphicerus sharpei</i>	(Branch 1991)
Reedbuck	<i>Redunca arundinum</i>	(Broadley 1983)
Common duiker	<i>Sylvicapra grimmia</i>	(Branch 1991; Alexander 2007)
Greater canerat	<i>Thryonomys swinderianus</i>	(Dixon 1966)
Nyala	<i>Tragelaphus angasii</i>	(Dixon 1966)
Sitatunga	<i>Tragelaphus spekii</i>	(Broadley 1983)
Bushbuck	<i>Tragelaphus sylvaticus</i>	(Broadley 1966)
Human “A”	<i>Homo sapiens</i>	(Branch and Haacke 1980)
Kudu “A”	<i>Tragelaphus strepsiceros</i>	(Branch and Haacke 1980)
Birds		
Egyptian goose (eggs)	<i>Alopochen aegyptiaca</i>	(Alexander 2012)
Domestic chicken	<i>Gallus gallus</i>	(Fitzsimons 1919; Broadley 1966)
Helmeted guineafowl	<i>Numida meleagris</i>	(Broadley 1966)
Ring-necked dove	<i>Streptopelia capicola</i>	(Pitman 1962)
Red-eyed dove	<i>Streptopelia semitorquata</i>	(Pitman 1962)
Reptiles		
Nile crocodile	<i>Crocodylus niloticus</i>	(Branch 1998)
Rock monitor	<i>Varanus albigularis</i>	(Broadley 1966)
Nile monitor	<i>Varanus niloticus</i>	(Broadley 1966)
Fish		
Cichlids	<i>Cichlidae</i>	(Bruton and Cooper 1980)
Sharptooth catfish	<i>Clarias gariepinus</i>	(Branch 1991)

Table 3.2: Prey species of southern African python sourced from social media up until 01 May 2024.

Common name	Latin name	Number of records	%
Mammals			
Impala	<i>Aepyceros melampus</i>	43	30.7
Springbok	<i>Antidorcas marsupialis</i>	1	0.7
Domestic cow	<i>Bos taurus</i>	2	1.4
Domestic dog	<i>Canis lupus familiaris</i>	5	3.6
Domestic goat	<i>Capra aegagrus hircus</i>	6	4.3
Red duiker	<i>Cephalophus natalensis</i>	1	0.7
Vervet monkey	<i>Chlorocebus pygerythrus</i>	7	5.0
African civet cat	<i>Civettictis civetta</i>	1	0.7
Blue wildebeest	<i>Connochaetes taurinus</i>	1	0.7
Domestic cat	<i>Felis catus</i>	1	0.7
Cape porcupine	<i>Hystrix africaeaustralis</i>	5	3.6
Waterbuck	<i>Kobus ellipsiprymnus</i>	2	1.4
Red lechwe	<i>Kobus leche</i>	3	2.1
Puku	<i>Kobus vardonii</i>	1	0.7
Scrub hare	<i>Lepus saxatilis</i>	4	2.9
Black-backed jackal	<i>Lupulella mesomelas</i>	3	2.1
Wild dog	<i>Lycaon pictus</i>	1	0.7
Banded mongoose	<i>Mungos mungo</i>	1	0.7
Klipspringer	<i>Oreotragus oreotragus</i>	1	0.7
Domestic rabbit	<i>Oryctolagus cuniculus domesticus</i>	6	4.3
Bat-eared fox	<i>Otocyon megalotis</i>	1	0.7
Domestic sheep	<i>Ovis aries</i>	3	2.1

Olive baboon	<i>Papio anubis</i>	1	0.7
Chacma baboon	<i>Papio ursinus</i>	1	0.7
Tree squirrel	<i>Paraxerus cepapi</i>	4	2.9
Springhare	<i>Pedetes capensis</i>	1	0.7
Common warthog	<i>Phacochoerus africanus</i>	2	1.4
Blue duiker	<i>Philantomba monticola</i>	1	0.7
Steenbok	<i>Raphicerus campestris</i>	3	2.1
Sharpe's grysbok	<i>Raphicerus sharpei</i>	2	1.4
Brown rat	<i>Rattus norvegicus</i>	2	1.4
Egyptian fruit bat	<i>Rousettus aegyptiacus</i>	1	0.7
Common duiker	<i>Sylvicapra grimmia</i>	7	5.0
Nyala	<i>Tragelaphus angasii</i>	6	4.3
Bushbuck	<i>Tragelaphus sylvaticus</i>	9	6.4
Ground squirrel	<i>Xerus inauris</i>	1	0.7

Birds

Egyptian goose	<i>Alopochen aegyptiaca</i>	4	5.1
Domestic duck	<i>Anas platyrhynchos domesticus</i>	1	1.3
Domestic goose	<i>Anser anser</i>	1	1.3
Tawny eagle	<i>Aquila rapax</i>	1	1.3
Hadedda ibis	<i>Bostrychia hagedash</i>	1	1.3
Red-billed oxpecker	<i>Buphagus erythrorhynchus</i>	1	1.3
Lesser striped swallow	<i>Cecropis abyssinica</i>	1	1.3
Greater striped swallow	<i>Cecropis cucullata</i>	1	1.3
Lilac breasted roller	<i>Coracias caudatus</i>	2	2.6
European roller	<i>Coracias garrulus</i>	2	2.6

White-faced whistling duck	<i>Dendrocygna viduata</i>	1	1.3
Black-winged kite	<i>Elanus caeruleus</i>	1	1.3
Golden-breasted bunting	<i>Emberiza flaviventris</i>	1	1.3
Southern red bishop	<i>Euplectes orix</i>	1	1.3
Southern white-crowned shrike	<i>Eurocephalus anguitimens</i>	1	1.3
Domestic chicken	<i>Gallus gallus</i>	10	12.8
Brown-hooded kingfisher	<i>Halcyon albiventris</i>	1	1.3
Woodlands kingfisher	<i>Halcyon senegalensis</i>	3	3.8
Black-bellied starling	<i>Lamprotornis corruscus</i>	1	1.3
Glossy starling	<i>Lamprotornis nitens</i>	6	7.7
Swallow-tailed bee-eater	<i>Merops hirundineus</i>	1	1.3
Yellow-billed kite	<i>Milvus aegyptius</i>	1	1.3
Helmeted guineafowl	<i>Numida meleagris</i>	3	3.8
Namaqua dove	<i>Oena capensis</i>	1	1.3
Greater flamingo	<i>Phoenicopterus roseus</i>	1	1.3
Spurwing goose	<i>Plectropterus gambensis</i>	1	1.3
White-helmet shrike	<i>Prionops plumatus</i>	1	1.3
Dark-capped bulbul	<i>Pycnonotus tricolor</i>	2	2.6
Green-winged pytilia	<i>Pytilia melba</i>	1	1.3
Laughing dove	<i>Spilopelia senegalensis</i>	8	10.3
Little tern	<i>Sternula albifrons</i>	1	1.3
Ring-necked dove	<i>Streptopelia capicola</i>	4	5.1
Bateleur	<i>Terathopius ecaudatus</i>	1	1.3
Damara red billed hornbill	<i>Tockus damarensis</i>	1	1.3
Southern yellow-billed hornbill	<i>Tockus leucomelas</i>	3	3.8

Southern red-billed hornbill	<i>Tockus rufirostris</i>	2	2.6
Green pigeon	<i>Treron calvus</i>	1	1.3
Emerald spotted wood dove	<i>Turtur chalcospilos</i>	2	2.6
Barn owl	<i>Tyto alba</i>	1	1.3
Cape white-eye	<i>Zosterops virens</i>	1	1.3

Reptiles

Nile crocodile	<i>Crocodylus niloticus</i>	1	50
Rock monitor	<i>Varanus albigularis</i>	1	50

Table 3.3: Prey species of southern African python added through personal observations.

Common name	Latin name	Source
Mammals		
Guinea pig	<i>Cavia porcellus</i>	K. Kyle
Harvey's duiker	<i>Cephalophus harveyi</i>	A. Martin
Samango monkey	<i>Cercopithecus albogularis</i>	R. & D. Kyle
Giant rat	<i>Cricetomys gambianus</i>	A. Martin
Rusty-spotted genet	<i>Genetta maculata</i>	A. Martin
Roan antelope	<i>Hippotragus equinus</i>	W. Whitfield
Yellow baboon	<i>Papio cynocephalus</i>	A. Martin
Laboratory rat*	<i>Rattus norvegicus</i>	K. Kyle
Lesser cane rat	<i>Thryonomys gregorianus</i>	A. Martin
Birds		
Southern ground hornbill	<i>Buvorcus leadbeateri</i>	A. Martin
Fantail pigeon	<i>Columba livia</i>	W. Whitfield
Sociable Weaver	<i>Philetairus socius</i>	R. & D. Kyle
Eastern golden weaver	<i>Ploceus subaureus</i>	K. Kyle
Double-banded sandgrouse	<i>Pterocles bicinctus</i>	R. & D. Kyle
Namaqua sandgrouse	<i>Pterocles namaqua</i>	R. & D. Kyle
Red-billed quelea	<i>Quelea quelea</i>	R. & D. Kyle

*Note this was preyed on by a wild python from a domestic rat colony

Of the 238 records of the southern African python diet we found on social media, 35 involved domestic animals of nine species, predominantly mammals (65.7%, Table 3.2). All of these incidents involved pythons of over 1.5 m, with 48.5% of the records involving pythons between 1.5 m and 3 m, and the remaining 51.4% involved pythons larger than 3 m.

In the social media records, we found 140 incidents of southern African pythons feeding on mammals. These feeding records were distributed across six mammalian orders, with Artiodactyls accounting for 67.1% ($n = 94$) of the records, Carnivora accounting for 9.3% ($n = 13$), and the remaining 23.6% being distributed amongst the remaining four orders (Figure 3.2a). There was a significant difference among the mammal orders preyed on, with Artiodactyls being consumed significantly more than the other orders ($\chi^2 = 16.46$, $df = 1$, $p < 0.001$).

There were 94 social media feeding records of southern African pythons involving birds, 90 of which were identifiable to at least the level of order. The majority of these birds (48.8%, $n = 44$) were from the Passeriformes order, with Galliformes accounting for the second largest percentage (15.5%, $n = 14$) and the remaining 35.5% ($n = 32$) distributed between the remaining eight orders as illustrated in Figure 3.2b. While there was a notable difference among the avian orders preyed on, with Passeriformes the most consumed, it was not significantly different ($\chi^2 = 0.04$, $df = 1$, $p = 0.833$).

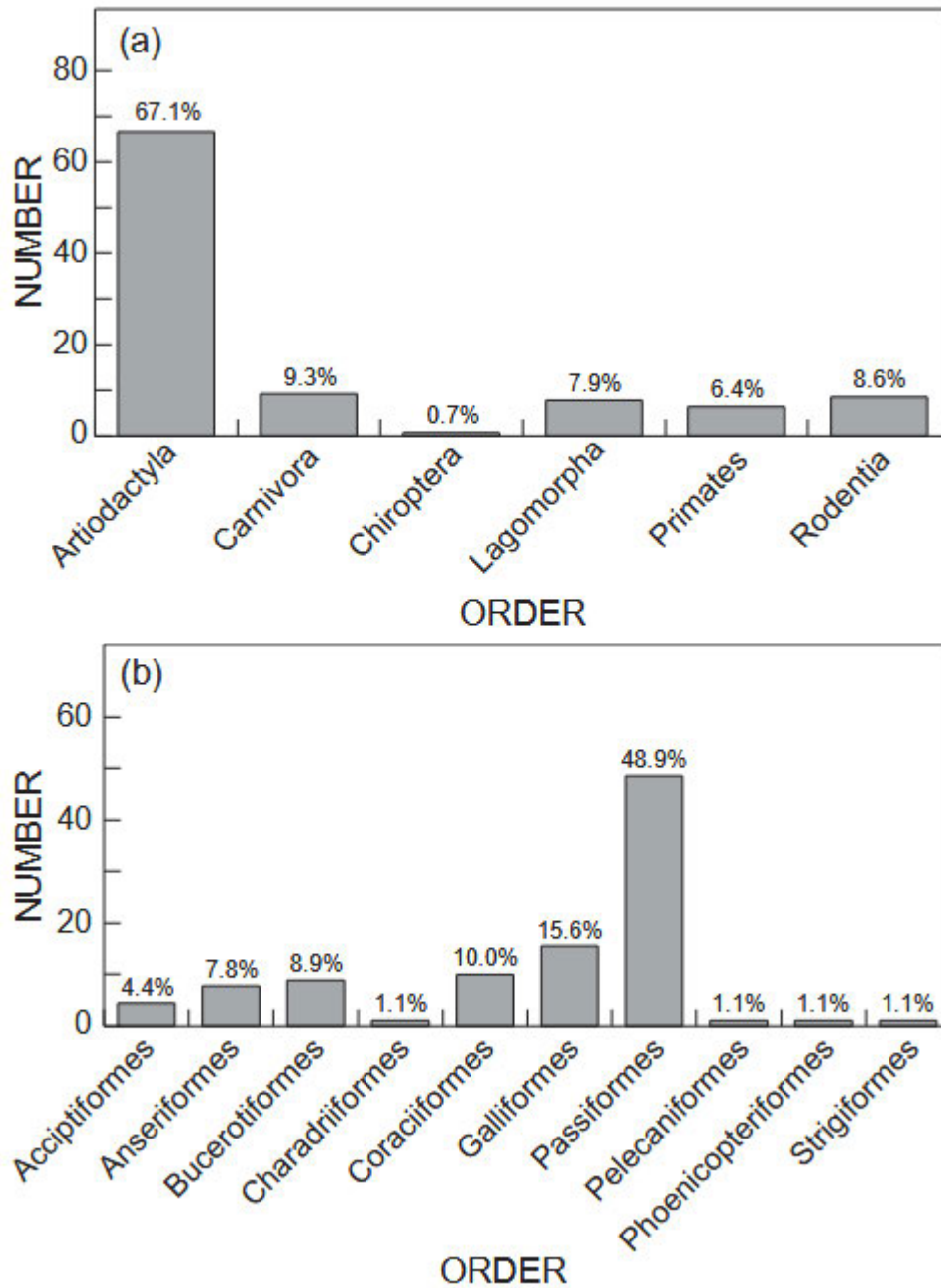


Figure 3.2: Percentage distribution of the feeding records of *Python natalensis* extracted off social media amongst a. mammalian, and b. avian orders up until 01 May 2024.

Analysis of the southern African python mammalian prey records from social media revealed that most of the species (44.4%) were only recorded once, with 16 single records (Table 3.2). However, the maximum number of individuals of a particular species recorded was impala (*Aepyceros melampus*), with 44 incidents recorded. This resulted in a mean of 3.8, while the mode was 1 and the median 2, indicating that the high incidence of impala in the records were an outlier and influenced the mean.

Considering the size classes of the prey records from social media, the medium-sized southern African pythons were found to have the most diverse diet ($H' \approx 0.83$) compared with the small pythons ($H' \approx 0.34$) and the big pythons ($H' \approx 0.28$). Of the mammalian records, 4.3% ($n = 6$) of the records were for small pythons, 29.3% ($n = 41$) involved medium-sized individuals, and the remaining 66.4% ($n = 93$) were all pythons of over 3 m (Figure 3.2). Of the avian predation records, only six feeding observations involved large pythons; the other 88 records were small pythons (52.1%, $n = 49$) or medium sized pythons (41.4%, $n = 39$). Considering the pythons in the 'large' category that were recorded, four involved domesticated animals where the southern African pythons were raiding farmyards, one involved a wild-caught spurwing goose (*Plectropterus gambensis*), and another a wild-caught greater flamingo (*Phoenicopterus roseus*). The pythons in the 'small' category had significantly more avian prey than mammalian prey ($\chi^2 = 33.62$, $df = 1$, $p < 0.001$), while the pythons in the 'large' category had significantly more mammalian than avian prey ($\chi^2 = 75.47$, $df = 1$, $p < 0.001$). There was no significant difference ($\chi^2 = 0.05$, $df = 1$, $p = 0.823$) for the medium-sized pythons.

Of the 55 southern African python social media feeding records where the snake was less than 1.5 m in length, 49 were events that involved birds. This showed that 89.0% of these feeding records for smaller pythons consisted of avian prey (Figure 3.2). In comparison, 48.7% of the

medium-length pythons' diet was avian species, and only 6.1 % of the largest pythons' diet was avian. This suggests that the pythons' diet changes as they mature, with a considerably larger proportion of their diet being avian as younger and smaller pythons than when they mature (Figure 3.3).

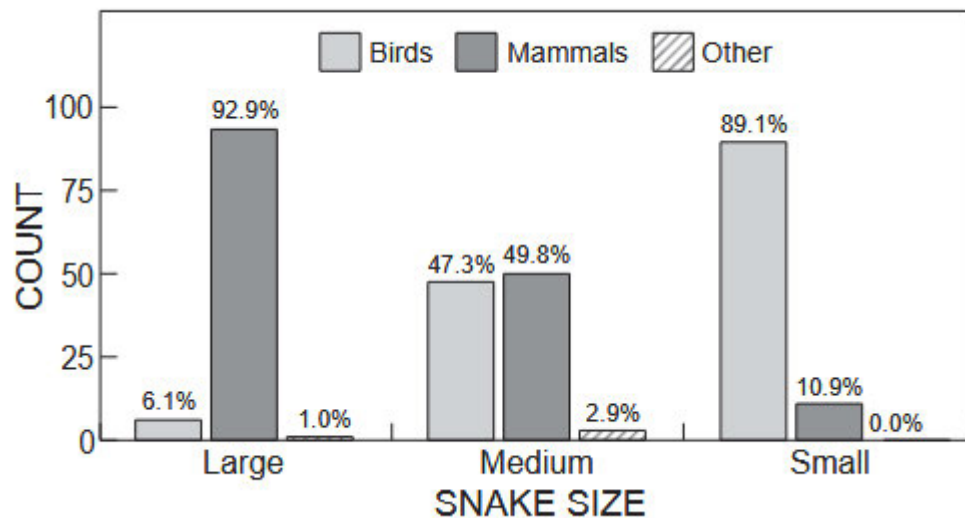


Figure 3.3: Percentage frequency distribution of the feeding records according to the size of the southern African pythons from the data extracted from social media.

3.3.3 Behaviour

From the social media records, it was possible to conclude that two individual southern African pythons had specialised in hunting birds. One was on a live webcam, where, on nine occasions, it was possible to see a python of a similar size lying on the same branch of a dead tree in full view of the camera. This python was assumed to be the same animal and was recorded taking nine different birds. A second similar instance occurred in a wildlife-friendly housing estate, where a smaller python was observed frequenting the same tree over a period of seven months. It was

observed feeding on six different avian species. Four records also came from similar-sized pythons feeding on birds in a hide in Mkuze Game Reserve, KwaZulu-Natal, South Africa. Finally, a young southern African python resident in a garden in Richard's Bay, KwaZulu-Natal, South Africa, was observed hunting at a water feature for at least three months. Four incidents were recorded of it capturing and eating small birds coming to the water feature, and could be identified as the same individual from its markings.

There were also historical records of southern African pythons in Etosha National Park in Namibia, consistently taking doves and other birds at artificial water holes (R Kyle and D Kyle pers. comm.; C Downs pers. obs.). This occurred several times at two waterholes during an extended period while two of the observers were stationed at the park.

A young southern African python of less than 1.5 m feeding on a little tern (*Sternula albifrons*) was observed at Kosi Bay, KwaZulu-Natal (26°57'20.909" S, 32°51'12.413"E; K Kyle pers. obs.). Between hunting forays, the terns roosted on branches used as fences in the traditional fish traps on the edge of Lake Nhlangwe. It was predicted that the python must have swum ± 150 m from the shore to the exposed branches to catch one of these terns which had returned to the roost.

Incidents of southern African python were also recorded during a study on an Egyptian fruit bat (*Rousettus aegyptiacus*) colony in KwaZulu-Natal, South Africa (Low De Vries pers. comm.; 9 January 2018). On several occasions, a southern African python was observed feeding on the bats in the cave, eating up to seven in one evening.

An incident was reported where a fisherman, using a large piece of chicken breast as bait while fishing for sharptooth catfish (*Clarias gariepinus*) in a river, reeled in a large southern African python hooked in the mouth (G Alexander pers. comm.). It was deduced that the python had found and eaten the bait while underwater.

A medium-sized (1.5–2 m) southern African python that was kept briefly in captivity before being released was observed caudal luring (K Kyle pers. obs.). The python was contained in a large glass terrarium while domestic chickens (*Gallus gallus*) ranged freely nearby. The python was lying in an ambush position when it began wriggling the conspicuously marked end of its tail in an undulating fashion. The chicken noticed this and advanced on the twitching tail from several metres away. The python remained completely motionless except for the continued movement of the tail tip. The glass tank prevented a successful feeding event, but the python's behaviour suggested its intentions were to lure a meal.

3.5 Discussion

Social media proved to be a useful tool for accessing large quantities of raw data, which was processed to reveal valuable information and insights into the diet of the southern African python. A list of 104 different species of animals as prey items was established, encompassing mammals, birds, reptiles and fish. Some interesting feeding observations were also discovered, including the targeting of avian prey and the consumption of bird eggs, as well as the hunting and consumption of fish underwater, and scavenging, which are atypical feeding strategies used by these predominantly ambush predators.

3.5.1 Ontogenetic shift in diet

Of the small-sized southern African python feeding records, 89.1% consisted of avian prey. Compared with 48.8% of the medium-length pythons' diet, and only 6.1% of the largest pythons' diet consisting of birds, it appears pythons exhibit an ontogenetic shift in diet from primarily consuming avian to mammalian prey as they grow in size, a trend that is mentioned by Jacobsen

(2005). This is likely due to the size and availability of prey. Birds are a readily available food source at water points and can provide fairly consistent meals for smaller pythons; larger pythons can take much bigger meals in the form of mammals, which would be less frequently caught but are likely more energy rich meals, making them preferable to the larger pythons, which are capable of hunting larger prey items. Considering the nature of the meals, there will also be a bias in the data available. For the larger pythons, consuming small bird meals would take little time. In contrast, larger mammalian meals will take considerably longer to swallow, making them more likely to be seen, photographed, and posted online than small, quick bird meals.

3.5.2 Hunting strategies

The described incidents where individual southern African pythons repeatedly used the same branches for hunting and displayed consistent hunting techniques imply that the smaller pythons focus on avian species. The bat cave and tern roost suggest that the pythons observed the behaviour patterns of the prey items (frequently returning to the same location) and intentionally situated themselves in places to benefit from this. Many of the larger southern African pythons' records show prey taken at watering holes or troughs, which suggests that the larger pythons still perform this focussed behaviour, just on mammals rather than birds.

The historical and social media records of southern African pythons consuming bird eggs reveal a different feeding technique from catching and constricting prey. It is possible that the pythons may have come across the nests coincidentally rather than hunting for them. The pythons that were caught in the fish traps in Lake Sibaya (Bruton and Cooper 1980) had entered the traps, eaten fish from the traps, and drowned therein because of the traps being submerged, meaning that they caught and consumed the fish underwater. This is reflected again in the account of the

fisherman who caught the python underwater using bait. Interestingly, the latter incident also confirmed their opportunistic scavenging techniques, which have been observed in captivity (various pers. obs.), but not previously confirmed in the wild.

In addition, the feeding on livestock kept in kraals or poultry in coops indicated that they move to places where animals are routinely kept, and actively feed on them. Past literature depicts southern African pythons as ambush foragers, waiting on game trails or close to water and in other convenient locations to intercept and catch suitable prey items (Broadley 1983; Branch 1998; Secor and Ott 2007; Marais and Kemp 2022). However, from the observed egg, fish, bird and livestock feeding behaviour, as well as the scavenging record, it appears that southern African pythons can use different hunting techniques, including active foraging and scavenging, confirming Alexander's (2012) suggestion.

3.5.3 Caudal luring

Caudal luring is a hunting strategy that some ambush foraging snakes use with either atypical tail colouration or behaviour to lure prey within striking range (Hagman et al. 2008). This technique had not previously been documented in southern African pythons, which have conspicuous colouration on the underside of the end of their tails, with the top continuing the camouflaged pattern of the rest of the body, while the underside has bold black and white markings. Instead, southern African pythons have been known to use their tails for defence (Greene 1973; Branch 2016). This was confirmed in social media predation records, with several videos and photographs of southern African pythons using a tail threat display whilst under attack from various predators. Caudal luring has been documented in some other species of pythons (Murphy et al. 1978), and as such, it is not surprising that southern African pythons also employ this hunting strategy.

Evidently, the conspicuously coloured tail-tip can be used for more than one purpose, and it is suggested that other species with this colouration could possibly also use this hunting strategy.

3.5.4 Domestic incidents

In a recent study based on human-wildlife conflict in Zimbabwe between local communities and southern African pythons, it became clear that the relationship between python age/size and the degree of this contribution in python-human conflicts needs to be understood for the sustainable conservation of pythons (Dube and Kavhu 2022). From the data gathered, it is apparent that the larger southern African pythons are responsible for the livestock taken. This has implications for human-python conflict. The presence of larger pythons implies the presence of smaller pythons; however, the lack of evidence of smaller pythons being documented raiding stock suggests that they are finding other prey sources, for example, rodents, around these human habitations and in their croplands, thus providing a valuable service rather than causing harm. Southern African pythons are known for the ecosystem services they provide to farmers in controlling pest numbers, especially greater cane rats (*Thryonomys swinderianus*), rock hyrax (*Procavia capensis*) (Branch 1998) and primate species. Unfortunately, the southern African python only reaches maturity at larger sizes, and thus, the killing or removing of many of the large individuals, which provide the recruitment, from these areas will result in a decline in the population and, thus, a concomitant reduction in the ecosystem services provided by the species.

3.5.5 Use of social media

It is difficult to quantify historical data when it comes to the diets of snakes, as many are broad suggestions, for example, ‘small antelope, wild pigs, monkeys and birds, particularly of the

ground-dwelling type' (Broadley, 1983, p.66). As such, it is challenging to pinpoint exactly which species were included. There are also several historical records which document attempted predations, where the prey item was killed, but not eaten, including, for example, a kudu (*Tragelaphus strepsiceros*) and a human, as well as an instance where southern African pythons were observed attempting to hunt sharptooth catfish (*Clarias gariepinus*). Pythons have typically been considered generalist and opportunistic predators. Our data collected from social media added 78 species of birds, mammals and reptiles to the known prey of southern African pythons, thus providing more evidence for their broad diets (Table 3.2).

Because the southern African python is a large, charismatic species, most people posting python pictures, or their commenters, identify them accurately, thus rendering the search word “python” effective. In comparison, nondescript species could not be successfully searched for in this manner. This is not a comprehensive survey of social media, but rather a use of the tools available to gather as much information as is easily accessible and available. While there were limitations to the amount of information that could be extracted from these records, amidst much misinformation, the amount of useful data and information that could be extracted from this method of data collection was surprising. Taking into account from the outset that this would not be a comprehensive search, the data were collected with the aim of gathering as much information as possible, with each record adding depth and value to the study. For a comprehensive search, specific programs could be used to find all mentions of certain search words; however, this is a much more complicated and time-consuming method, while the approach we used was much simpler and sufficient for this study.

Our social media data showed that Facebook® accounted for the vast majority of the southern African python records. This is likely due to reasons such as the ‘users’ demographics,

the prevalence of ‘sightings pages’, the layout of the posts and the ease of searching on this platform. On the assumption that older members of the population are more likely to be spending time in nature and that Facebook® is a more popular platform among older generations, it followed that this would be the most fruitful platform for records. Its search options also made it more user-friendly for accessing different ‘python’ posts, while other platforms were more limiting. There is also a prevalence of ‘couch naturalists’ who spend a lot of time browsing social media for what they think is relevant information and re-posting it to certain pages, which allows for much easier access for researchers. These are all features that make Facebook® a more user-friendly platform for accessing and extracting data (Hausmann et al. 2017, 2018).

The distribution of the records, with the majority coming from South Africa, can be explained by the number of people likely to post pictures on social media, especially Facebook®, from different countries (Hausmann et al. 2017, 2018). Most of the social media records came from snake identification groups or sighting groups from game reserves. South Africa has a considerably larger population group that is likely to post on these groups. South Africa also has a large area with suitable habitat and, therefore, most likely a larger population of pythons than several of the countries, for example, Namibia. Within South Africa, Limpopo province had the largest number of records, which is accounted for mainly by Kruger National Park, with several others from the surrounding lodges and reserves. While Kruger National Park is a vast natural area, many tourists are constantly moving through it, searching for interesting sightings and likely to post them (Hausmann et al. 2017, 2018). These factors should be considered when designing a study like this.

While social media is not the answer to all data collection problems and questions, it was beneficial and rendered an impressive amount of useful data in this study. As mentioned

previously, detailed behavioural studies demand unrealistic amounts of time, resources and effort. By contrast, social media provides researchers with an extensive resource for extracting varied information that can be collated to provide fascinating and relevant clues and insights into rare, as well as common species. As a research method, it requires a reasonable amount of groundwork, as well as an understanding of the species and ecosystems in question, to be used effectively. However, with this in place, it can be an effective research tool.

3.6 Acknowledgements

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3.7 Data availability

The data belong to the University of KwaZulu-Natal and are available from the authors on reasonable request.

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3.9 Supplementary information



Supplementary information Figure S3.1. An image of a southern African python (*Python natalensis*). (Source: K. Kyle©)

Supplementary information Table S3.1. Examples of social media sites accessed on the Facebook platform for examples of southern African python (*Python natalensis*) diet

Facebook page	Link
Predation Records Reptiles and Frogs (Sub-Saharan Africa)	https://www.facebook.com/groups/888525291183325
Snakes of Southern Africa	https://www.facebook.com/groups/96621376042
Snakes and snakebite of Africa	https://www.facebook.com/groups/1643835265678127
Marloth Park Sightings Page	https://www.facebook.com/groups/377035355798904
Zambeze delta conservation and anti-poaching	https://www.facebook.com/search/top/?q=Zambeze%20delta%20conservation%20and%20anti-poaching%20
South Coast Herald	https://www.facebook.com/search/top/?q=South%20Coast%20Herald
Reptiles of Southern Africa	https://www.facebook.com/groups/ReptilesSouthernAfrica
Snakes and creepy crawlies of Malawi	https://www.facebook.com/groups/158862031304054
Snakes of Namibia	https://www.facebook.com/groups/187156948143224
Zambian snakes and other crawlies	https://www.facebook.com/groups/Zamsnakes
Birding in Africa	https://www.facebook.com/groups/birdinginafrica
Birds of Zululand	https://www.facebook.com/groups/birdsofzululand.kzn
Hluhluwe-Imfolozi sightings	https://www.facebook.com/groups/hluhluweimfolozisightings
KNP- Best place on Earth	https://www.facebook.com/groups/krugerparkearth
Kruger National Park - the best of Kruger	https://www.facebook.com/groups/kruger.national.park.the.best.place.on.earth
Latest sightings - Kruger	https://www.facebook.com/search/top/?q=Latest%20sightings%20-%20Kruger
Parks and Wildlife- Zululand	https://www.facebook.com/groups/1486062508328147
SA birds, birders and birding	https://www.facebook.com/search/top/?q=SA%20birds%20C%20birders%20and%20birding
Tembe Elephant Park	https://www.facebook.com/TembeElephantPark
Wild snake predation records	https://www.facebook.com/groups/wild.snake.predation.records

CHAPTER 4

Beautifully dangerous or dangerously beautiful: Indigenous knowledge and perceptions of southern African pythons (*Python natalensis*) in southern African rural and urban areas

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Running header: Indigenous knowledge and perceptions of southern African pythons

4.1 Abstract

Background Snakes are a group of vertebrates that evoke strong feelings and generate much interest. Southern African Pythons (*Python natalensis*) are the largest snake species in Southern Africa, providing substantial ecosystem services, but also negatively impacting people by consuming their livestock and pets. Our study aimed to assess the attitudes of South Africans towards southern African pythons, and to analyse what might influence either a positive or a negative attitude towards them. This is important because of the significant persecution this species is presently facing, as well as its declining population trend.

Methods In 2023, 2024, and early 2025, we employed a mixed-model approach that combined face-to-face interviews to complete the questionnaire, and an electronic online version that could be completed by respondents, to investigate the perceptions and attitudes of people towards pythons in South Africa, particularly in KwaZulu-Natal Province. This resulted in 438 responses from diverse demographic and geographic backgrounds, which we then analysed to better understand how South Africans view these snakes.

Results The results were not as predicted, with a significant majority having an overall positive attitude towards these snakes. Valuable insights into the cultural significance of pythons and how this trend is evolving over time were obtained, as well as some insight into the misinformation surrounding this species and the factors that influence these perceptions. We also assessed superstitions involving pythons, as well as traditional medicine (*muthi*) uses, and how people perceived pythons to be dangerous.

Conclusions While the general attitude towards pythons appeared to be positive, there was a concerning element of misinformation as well as persecution, and we suggest that efforts be made to educate and inform people wherever possible.

Keywords: Snakes, Reptiles, Questionnaire, Citizen Science.

4.2 Introduction

Snakes evoke strong feelings in humans - good and bad - with few people remaining neutral towards them [1]. Literature suggests that the fear of snakes is innate and even helps form the mammalian fear response; however, studies also show that there is a learned component to this fear [2, 3]. Snakes are steeped in mythology and have connotations worldwide in many different cultures and religions, ranging from being considered sacred to having divine status and being worthy of worship [3, 4, 5]. They hold a complex place in culture, representing many different things; for example, in the Bible, they represent wisdom, evil and an agent for God's vengeance [6]. In many myths surrounding snakes, they are portrayed in a negative light as harmful creatures, but this is seldom based on their natural history; rather, it is often the result of unnatural acts, driven by human fear, emotion, and assumption [3].

Different snakes hold similar relevance and meaning across different cultures and religions. The rattlesnake (family Crotalinae) in America and the python (*Python* spp.) in Africa are both associated with reincarnated ancestors, while snakes in general are associated with reincarnation for Hindus and are considered the “guardians of life” [3, 7, 8]. They are also strongly linked to weather and rainfall in many cultures worldwide, spanning across Asia, America, and Africa [3]. There are also some positive connotations associated with snakes, such as their representation of health, life, and good fortune, a sentiment echoed in African folklore and myths [9]. In the Bible, they are also associated with healing, as in American and African folklore [10]. Demographic aspects such as gender and level of education are known to impact these fears, with women being more scared than men and less educated people being more scared than those with higher levels of

education [11, 12]. Although these myths and beliefs often originate from fear and ignorance, they can be dispelled through education [3]. Furthermore, the fear of snakes, regardless of its innate origins, can be overcome [1].

The southern African python (*Python natalensis*) (hereafter python) is the largest snake species in Africa [13]. It is listed as “Least Concern” in the latest Red Data List because of its extensive and possibly expanding range, although several populations have become locally extinct, and the overall population trend is declining [14]. Known anthropogenic threats include residential and commercial development, agriculture, electric fences, being killed to protect livestock, and harvesting for traditional medicine (*muthi*), as well as for meat, skins, and the pet trade [8, 14, 15, 16, 17, 18]. They are protected under the National Environmental Biodiversity Act, 2004 (Act No. 10 of 2004): List of Terrestrial and Freshwater Species (ToPS list) in South Africa. According to the IUCN listing, the recommended conservation measures would be to quantify their use in the *muthi* trade and define their home range and requirements [18]. *Muthi* is the isiZulu word for a substance, which can contain animal or plant material and can have either spiritual or medicinal use [19], it can be used for various outcomes, ranging from healing, cleansing and protection from evil forces, to witchcraft and the infliction of curses and ill-health [20].

Southern African pythons are fond of water, often spending long periods largely submerged, especially after feeding or before sloughing, and frequently hunt from submerged positions in water [21]. They have large teeth and lunge and bite readily in defence, inflicting large, ripping wounds that bleed profusely [22]. They are the only southern African snake species that grow large enough to consider humans as prey. While there are no confirmed records of pythons consuming humans, fatalities have been reported [23].

According to a small study of 120 isiZulu respondents across a broad spectrum of age groups in 2016, snakes are the most feared animal, with 98% of respondents being scared of them [24]. In the literature, pythons are associated with much superstition by tribes in many parts of Africa [9, 25]. In some regions, they are considered a delicacy and are intentionally hunted down for food [26, 27]. Some revere and protect them as repositories for departed souls or the pets of witch doctors [9, 28], while still others believe that their fat works as a lubricant for rheumatism and can heal chest pains. Their internal organs have other medicinal uses [8]. In some cultures, they are revered for their proposed connection to water and rainfall; in others, they are sacrificed to induce rainfall events [25]. Whether spiritual, medical or simply as food, pythons are important in African societies and feature extensively in folklore and legend [9, 25, 27].

As so little is known about the beliefs, uses and attitudes towards these snakes, it is unclear what can be done to alleviate the culturally induced threats that they face. Our study aimed to assess the attitudes of people in southern Africa towards southern African pythons and to analyse what might influence either a positive or negative attitude towards pythons. These included the following: To assess if exposure to pythons influences attitudes towards these snakes; to establish the overall opinion of the public towards pythons and to assess how accurate the general perceptions of the negative and positive impacts of pythons are; to attempt to clarify some of the traditional beliefs around pythons and their uses in *muthi* and culture and to establish if this is still believed to the same extent as it was historically. Finally, we aimed to gather anecdotal information on breeding behaviour and burrow use from respondents that would likely not otherwise be documented. We predicted that there would be negative perceptions towards these snakes. Armed with the knowledge from this and similar studies, informed management and policy decisions can be made that can offer more relevant protection for this species.

4.3 Methods

4.3.1 Study area

The majority of the in-person interviews were conducted by an isiZulu-speaking individual conducting interviews in the Ongoye area of KwaZulu-Natal Province, South Africa. Interviews were also conducted in Manguzi, Umkhanyakude District Municipality, and opportunistically in Pietermaritzburg and Hilton, KwaZulu-Natal. The questionnaires were opportunistically deployed, with focused in-person questionnaire sessions conducted in concurrence with other similar studies. Additionally, individuals from southern Africa who could or preferred to complete the questionnaire online did so. As such, the results provide a broad representation of the responses from people from southern Africa, rather than any specific group. The use of in-person interviews and online platforms allowed for a wider range and broader engagement with respondents.

4.3.2 Data collection

We designed a questionnaire (Supplementary information Table S4.1), which was granted permission by the University of KwaZulu-Natal Humanities Ethics Committee (HSSREC/00006162/2023) to be completed by individuals over the age of 18 who had agreed to the consent form (Supplementary information Table S4.2). The questionnaire was divided into five sections, gathering data on the respondents' demographics, perceptions of pythons in relation to people, knowledge of python distribution and populations, python burrow use and breeding/social behaviour and, finally, python diet. Each section included a selection of multiple-choice questions, short-answer questions, or Likert scale questions. The questionnaire was translated into isiZulu, the predominant local language in KwaZulu-Natal, where most of the responses originated, and

respondents were allowed to fill it out in their preferred language. Additionally, the questionnaire was formatted for online completion using Google Forms®.

The questionnaire's online link was distributed as widely as possible through various platforms, including Facebook®, WhatsApp®, email, and printed flyers with QR code links to the Google Form® to encourage people from southern Africa to complete the questionnaire online. Likely Facebook® groups and pages were targeted, for example, "Snakes of Southern Africa" and other snake-related pages. Additionally, we distributed using mailing lists to likely participants, for example, the KwaZulu-Natal Conservancies network. Flyers with the link to the online questionnaire were distributed in likely areas to attract respondents, including tourism resorts and town notice boards.

4.3.3 Statistical analyses

A subset of questions from the questionnaire were posed as Likert scale questions. These questions typically ranged from four to five points, from very positive to very negative, or from strongly agree to strongly disagree, and were useful for gauging feelings around a topic where simple yes-or-no answers did not offer much insight. The data derived from the Likert scale questions were all treated as ordinal.

We performed basic descriptive statistics using the base R Core package [29], including Chi-Squared tests for significance. We performed a multinomial logistic regression model from the "nnet" package in R to analyse the factors likely to affect the negative or positive attitudes of respondents. The predictors we used were age, gender, education, province, employment status, and whether they had previously encountered a python. We conducted a binary logistic regression analysis using 349 respondents who either held a negative or positive attitude towards pythons.

The independent variables we used were gender (male or female), age, level of education (school or tertiary), employment status (employed or unemployed), whether they lived within KwaZulu-Natal or not, and whether or not they had encountered a python. Graphics, including the Likert Scale heatmap, were created using the “ggplot” package in R, while “wordcloud2” was used for the word cloud.

4.4 Results

4.4.1 Demographics of respondents

The majority of the questionnaires were completed in late 2023 and early 2024, with a final batch prior to analyses in early 2025. The majority of the responses were collected through the online questionnaire, which was completed by respondents from all over South Africa, as well as several from outside the country, within the southern African python’s distribution range. A few respondents came from outside the distribution range but had spent time within it and had experienced encounters with these snakes.

A total of 438 responses were recorded for the questionnaire, comprising both online responses and in-person interviews. All of these responses were used for the analysis of this study; however, respondents did not answer all questions, resulting in varying numbers of responses for certain questions (as indicated in parentheses). These differences were accounted for by some people only partially filling out the questionnaire, and additionally, many of the questions were only relevant to individuals who had had specific encounters (for example, pythons feeding or pythons in burrows), cultures, or beliefs.

The respondents were almost equally split between males and females, with 51% females ($n = 225/438$) (Table 4.1). The dominant age group was 18 – 33 year olds ($n = 174$), followed by

34 – 49 year olds (n = 138), and finally the 50+ year olds (n = 129) (Table 4.1). The vast majority (84%, n = 368) of the responses were submitted via the online questionnaire form, while the remaining 16% (n = 70) were completed as hard copies in person. The majority were completed in English, while 20% were written in IsiZulu and translated for the analyses.

There was a significant difference between the education status of the respondents ($\chi^2 = 505.55$, df = 3, $p < 0.001$), with the majority of respondents having a tertiary education (67%, n = 294) (Table 4.1). Of the 141 people who responded to where they lived, significantly more lived in rural areas (62%, n = 87) ($\chi^2 = 51.447$, df = 2, $p < 0.001$). The 155 people who responded about home language differed significantly, with the majority being isiZulu speakers (n = 90). A significant majority of respondents (65%, n = 283) were employed. It is presumed that most of the students identified as unemployed. The majority of respondents came from KwaZulu-Natal (68%, n = 299), with the second highest coming from Gauteng Province (8%, n = 37), followed by Limpopo Province (8%, n = 34), and the remaining 16% being split between the remaining six provinces, outside of South Africa and those that left this blank.

Table 4.1: Demographics of the participants of the questionnaire in the present study.

Demographics		No. of respondents	Percentage (%)
Gender	Female	225	51.4
	Male	209	47.7
	Prefer not to say	3	0.7
	(blank)	1	0.2
Age	18-25	79	18.0
	26-33	95	21.7
	34-41	78	17.8
	42-49	60	13.7
	50+	126	28.8
Education	None	4	0.9
	Primary	14	3.2
	Secondary	118	26.9
	Tertiary	294	67.1
	(blank)	8	1.8
Urban/Rural	City	24	5.5
	Rural	87	19.9
	Town	30	6.8
	(blank)	297	67.8
Home language	Afrikaans	6	1.4
	English	57	13.0
	IsiZulu	90	20.5
	Siswati	1	0.2
	Venda	1	0.2
	(blank)	283	64.6
Employment	Employed	283	64.6
	Student	4	0.9
	Unemployed	147	33.6
	(blank)	4	0.9
Province	Eastern Cape	13	3.0
	Free State	1	0.2
	Gauteng	37	8.4
	KwaZulu Natal	299	68.3
	Limpopo	34	7.8
	Mpumalanga	9	2.1
	North-West	2	0.5
	Outside SA	24	5.5
	Western Cape	13	3.0
	(blank)	6	1.4

4.4.2 Attitudes, feelings, and perceptions of pythons

Regarding respondents' feelings towards southern African pythons, 9% (n = 41) were neutral, 19% (n = 82) were negative, and 65% (n = 285) were positive, while 7% (n = 30) did not respond. Of the negative responses, the majority were scared of pythons, using words like “fear” and “frightening” to describe them, one used “deadly”, while 24 (5%) thought they were “dangerous” and seven (2%) used the word “hate” to describe their feelings towards them. Of the neutral respondents, the word predominantly used to describe pythons was “misunderstood”, while others were “avoid”, “ignorant”, and “big” (Fig. 4.1). The most frequently used positive word to describe pythons was “beautiful”, with 58 (13%) uses, while “love” was used 49 (11%) times and “important” 45 (10%) times. “*Muthi*” was used to describe them positively six times (1%), while “good luck” was used five times (1%) to describe pythons. Several different words were used to appreciate their role in the environment, for example, “essential”, “important”, and “necessary”. Meanwhile, several others described their feelings towards them, such as “wonderful”, “special”, and “amazing”.



Figure 4.1: A word cloud of the overall feeling of participants towards pythons, where the size of the font used indicates how frequently it was used to describe the snake.

Our binary analyses generated a model that revealed several significant predictors, specifically age, with the 50+ age category ($OR = 9.75$, $p < 0.001$) having the highest likelihood of a positive attitude towards southern African pythons. Having encountered a python also significantly increased the likelihood of a positive attitude ($OR = 5.00$, $p < 0.001$). Additionally, respondents from outside KwaZulu-Natal were significantly more likely to have a positive attitude than those from within ($OR = 3.33$, $p = 0.004$). Unemployment also had a significant effect ($OR = 0.26$, $p < 0.001$), with individuals who were unemployed being significantly more likely to have a negative attitude towards pythons. Gender and education were found to have non-significant effects on the attitude of respondents. The model had an AIC of 270.67 and a residual deviance of 250.67, with a null deviance of 375.76. The summary of predictors is shown in Table 4.2.

Table 4.2: Summary of predictors for the binary regression model on respondents' attitudes to pythons.

Predictor	Coefficient (β)	Odds Ratio (OR)	p-value	Significance
(Intercept)	-0.5225	0.59	0.3183	
Age 26–33	0.9448	2.57	0.0413	*
Age 34–41	1.8610	6.43	0.0013	**
Age 42–49	1.0225	2.78	0.0516	.
Age 50+	2.2772	9.75	<0.001	***
Gender (Male)	0.1613	1.17	0.6255	
Education (Tertiary)	0.3446	1.41	0.3337	
Employment (Unemployed)	-1.3561	0.26	<0.001	***
Province (Outside)	1.2037	3.33	0.0040	**
Encountered (Yes)	1.6101	5.00	<0.001	***

Only a small subset of respondents provided information about their home language and whether they lived in rural or urban environments. Of the 74 people who responded that they lived rurally, 55% (n = 41) had a negative attitude to southern African pythons, while 9% (n = 7) were neutral and 35% (n = 26) were positive, while of the 53 respondents living in urban environments, 13% (n = 7) had a negative attitude while 11% (n = 6) were neutral and 75% (n = 40) were positive. We found a significant relationship between location and whether individuals were positive or negative towards pythons ($\chi^2 = 23.64$, $p < 0.001$). The rural participants were disproportionately represented in the negative category compared with the urban participants. A two-proportion z-

test revealed that rural respondents were significantly more likely to hold a negative attitude towards pythons than urban respondents ($p < 0.001$, 95% CI [0.277, 1.000]).

Regarding home language, of those who completed this question, the majority spoke isiZulu ($n = 63$), followed by English ($n = 56$), Afrikaans ($n = 6$), and Siswati and Venda, both with one respondent each. Of the 65 English home language speakers, 13% ($n = 7$) were negative, 7% ($n = 4$) were neutral, and 80% ($n = 45$) had a positive attitude towards southern African pythons. Of the 63 isiZulu home language speakers, 65% ($n = 41$) had a negative attitude, 11% ($n = 7$) were neutral, and 23% ($n = 15$) had a positive attitude. We found a significant association between language and attitude towards snakes ($\chi^2 = 53.09$, $p < 0.001$). IsiZulu home language speakers were disproportionately represented in the negative attitude category compared with speakers of other languages. A two-proportion z-test confirmed that isiZulu home language speakers were significantly more likely to have a negative sentiment than non-isiZulu home language speakers ($p < 0.001$, 95% CI [0.401, 1.000]).

When asked about the perceived positive impacts of southern African pythons, the dominant response was pest control, with 239 respondents (55%) identifying it as a benefit. Several combined it with other answers, for example, three combined ‘pest control’ with ‘income from selling the skins’. The second highest response was their importance in the food chain (13%, $n = 58$), which was similar to the pest control answer, but differed subtly in that their place in the food chain implies they are both an important prey item and a predator. The third highest response was that pythons have no positive impacts (13%, $n = 56$), and 25 respondents (6%) did not know if they did or not. Seven individuals (2%) recorded “*muthi*” as a positive impact, and 11 (3%) participants acknowledged the role of pythons in tourism as having a positive impact. Other interesting responses included six respondents (1%) who thought pythons ate harmful insects, two

who identified them as seed dispersers, and one who believed they improved soil health with their burrows.

Regarding the perceived negative impacts of southern African pythons, 189 (43%) respondents believed they posed a threat to livestock, with 40 (9%) expressing concern about both pets and livestock, and 32 (7%) worrying about the impact on humans and livestock. Multiple respondents (n = 101, 23%) did not think there were any negative impacts of pythons. Some respondents (13%, n = 58) believed pythons posed a threat to human beings, especially children. Few (6%, n = 25) respondents were concerned about their pets being eaten by pythons; pets differ from livestock, as livestock implies a livelihood, whereas pets are more associated with pleasure. Other unusual answers included two respondents who believed pythons carried diseases, three who thought they were invasive, two who thought they were poisonous, and three who thought they were magical.

When asked about the cultural significance of southern African pythons, only 97 respondents (22%) provided an answer, with 61 (14%) associating them with positive cultural experiences and 36 (8%) with negative ones. Some respondents (9%, n = 39) were unsure whether pythons were culturally important, while many (52%, n = 229) stated that pythons were not culturally important to them. Additionally, 65 respondents (15%) left this question blank. Few respondents (5%, n = 21) associated pythons with *muthi*, while eight (2%) believed that pythons have healing properties (the implication is through fat and oil, thus also *muthi*). Six (1%) people thought pythons were evil; one said pythons are bad luck, while another said killing pythons resulted in bad luck. Several beliefs were mentioned, including that pythons are invisible (n = 2), that pythons carry messages and prophecies, and that pythons bring strength, wisdom, fertility, and protection from evil spirits. Pythons were also associated with rain and water. There were several

references to their involvement with *Sangomas* (traditional healers acting in the roles of diviners and spiritual mediums); two referred to them as part of their initiation rites, others mentioned pythons as their pets, and others linked them to their ancestors. Few (1%, n = 4) participants linked them with fertility, and two (0.5%) mentioned rebirth and new beginnings associated with these snakes. There were five (1%) who associated pythons with witchcraft and one who thought pythons were a bad omen.

In relation to which parts of the southern African pythons were used for *muthi*, only 47 people (11%) responded. The most frequently mentioned part was the fat or oil from the python, with 36 mentions, followed by the skin, with 24 mentions (Table 4.3). Other parts mentioned included two accounts of the bones being used, and a single account of the skull, gallbladder, organs, and meat of pythons being used (Table 4.3). These were used to treat a wide array of physical and spiritual ailments. Of the 24 ailments for which python *muthi* was used, 12 (50%) were related to physical complaints, and 12 (50%) were for spiritual/emotional healing (Table 4.3). The most common physical ailment was general healing when the fat is spread over a wound, and the second most frequently mentioned was the treatment of ear infections (12.5%, n = 3). The spiritual connotations reported centred on power, protection from spirits, longevity, and wealth.

Table 4.3: Physical and spiritual ailment uses of southern African pythons and parts used in traditional medicine (*muthi*).

Use	Count	Parts	Count
Contacting ancestors	1	Bones	2
Courage	1	Fat	36
Diarrhea	2	Gall bladder	1
Ear infection	3	Meat	1
Healing	9	Organs	1
Longevity	1	Skin	24
Luck	1	Skull	1
Power	4		
Protection	1		
Protection - lightning	1		
Protection - spiritual	2		
Removes bad omens	1		
Spiritual ailments	1		
Swelling	2		
Wealth	1		

Regarding the question of whether the participants were aware of any specific superstitions involving southern African pythons, the answers were highly varied. There were 184 (42%) responses to this question; however, 83 (45%) of these indicated that the respondents were aware of superstitions, while 14 (8%) stated that they were not aware of any superstitions. Of the remaining 87 (47%) answers, there was a wide range of superstitions involving ancestors and luck, both positive and negative, others indicating that pythons were evil and demonic. Some specific superstitions related to southern African pythons, as reported by respondents, are detailed in Table 4.4.

Table 4.4: Superstitions and/ beliefs involving southern African pythons reported by some respondents.

Superstitions and/ beliefs about southern African pythons reported
Pythons use their spurs to block a human's nose in order to kill them
Burying a python skull under a kraal keeps the herd safe
Pythons cause a thunderstorm when they emerge from water
Pythons change colour
Pythons would not eat unweaned human babies because they smell like mothers' milk
Pythons are controlled by witches
Pythons can hypnotise people to eat them
People go blind having seen pythons
Pythons eat humans, particularly near water sources
Eating a python's gall bladder causes other snakes to fear you
Pythons bring money
Pythons are harbingers of death
The hook on the tail is to sweep your feet out from under you in order to eat you
If a python is killed, there will be no rain
Pythons can indicate pregnancy
A rainbow indicates that a python is bathing
Pythons use their tongues to suck out human brains
Pythons can transform into humans
White pythons live under waterfalls and can ensure good crops if sacrificed to
Humans go insane if they kill them.

Finally, when asked if there was a difference in the way people responded to southern African pythons depending on their age, the answers were varied: 5% did not answer, 16% were unsure, 24% did not think there was a difference, and 55% believed that there was a difference. Only 89 (20%) respondents clarified which age group they thought was more fearful, with 60 (67%) saying the older group was more scared, while 28 (31%) thought it was the younger group, and one said it was the children and elderly.

4.4.3 General views

We used a Likert scale for four questions. The first question was simply on a scale of positive to negative – the question being, “How do you view pythons?” Many respondents (46%) viewed them as purely positive, while 7% viewed them as purely negative. Most respondents (325 out of 438, 74%) were on the positive side of the scale, while 10% ($n = 44$) were neutral, and only 16% ($n = 69$) were negative (Fig. 4.2).

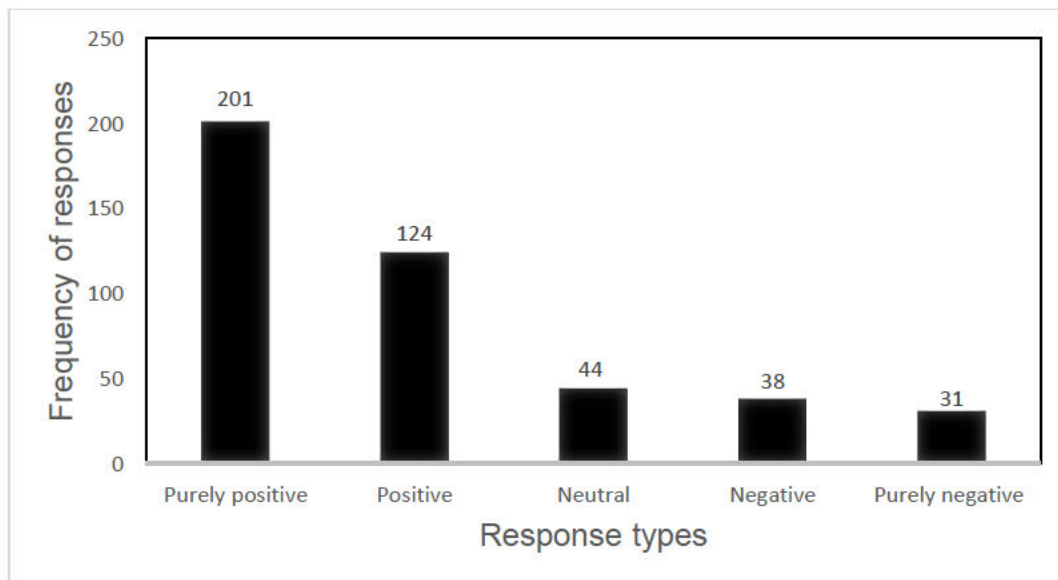


Figure 4.2: Frequency of responses of how people felt towards pythons in the present study.

When asked how they would respond to a python in close proximity to their homestead, the responses were mixed, with the most people (30%, $n = 130$) saying they would encourage it to be there, while 125 (29%) people would ignore it, 120 (27%) would chase it away but not kill it and only 61 (14%) would kill it immediately. When asked about their ability to identify pythons over other species of snakes, 63% ($n = 275$) were confident of their identification abilities, followed by 22% ($n = 96$) who were fairly confident they would identify it correctly. Few people

(8%, n = 36) were not confident in their identification, while 28 people (6%) were not confident at all and thought that all snakes look the same, and three refrained from answering.

The next question asked how dangerous the respondents thought pythons were to humans. Many (56%) thought that pythons were not dangerous to humans, while 17% thought they would get sick, but would recover quickly if bitten, 16% thought they were deadly, and 10% thought that you would get very sick, but would not die. This was linked to a follow-up question about whether respondents thought pythons ate humans. The responses to this question were less polarised, with 36% (n = 159) knowing that they did not, 26% (n = 118) thinking they could or had heard about it, 24% (n = 108) doubted that they could eat someone and 12% (n = 53) were convinced that they could. The responses to these four questions are summarised in Fig. 4.3.

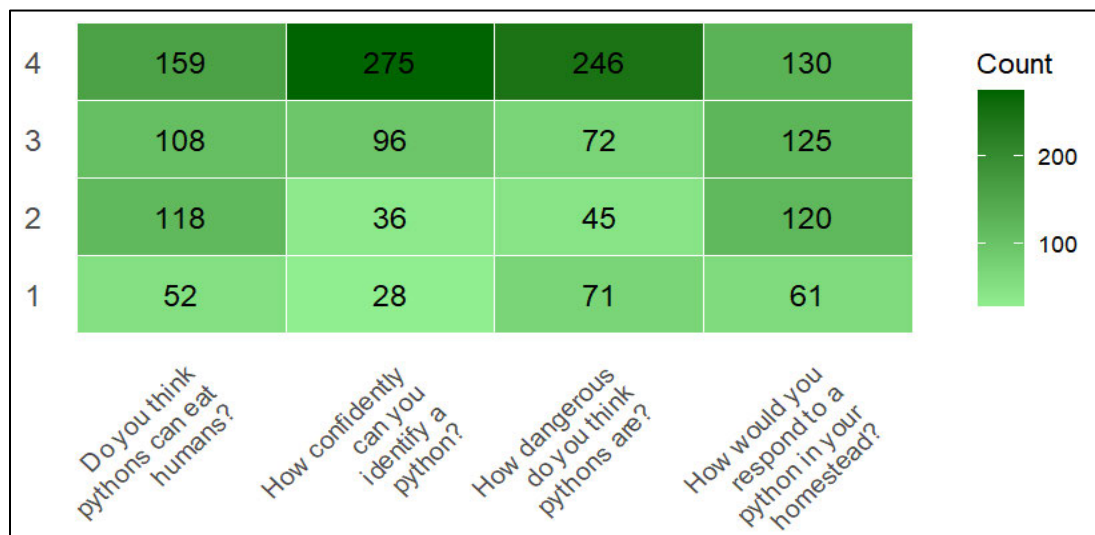


Figure 4.3: A heatmap of the responses from the four Likert scale questions about pythons. (Note: For question 1, the responses were 1 = definitely yes, 2 = I think they could or have heard about it happening, 3 = I doubt it, and 4 = I know they don't. For question 2, 1 = I'm absolutely certain I know exactly what they look like, 2 = I'm pretty sure I know what pythons look like, 3 = I'm not really confident, 4 = I'm not confident at all, they all look the same. For question 3, 1 = Absolutely

deadly, one bite will kill me, 2 = They are very dangerous, if bitten I will get sick, but I won't die, 3 = I will get sick but will recover, 4 = They are harmless to humans. For question 4, 1 = Kill it immediately, 2 = Chase it away but not necessarily kill it, 3 = Ignore it completely, 4 = Encourage it to be there).

The final two questions were comparing the past with recent sightings of pythons. While 111 participants (25%) thought they were seeing pythons as frequently as they did in the past, 20% felt that they were seeing pythons less frequently ($n = 88$), while 37% ($n=164$) were of the opinion that they were seeing pythons a lot less frequently than in the past. Only 26 respondents (6%) thought they saw pythons a lot more regularly than in the past, and 34 (8%) respondents thought they were slightly more frequently seen. The last question compared the size of pythons seen previously with those seen recently and showed that many respondents (46%, $n = 203$) believed that the pythons they had seen recently were similar in size to those in the past. Some (28%, $n = 116$) of the respondents believed the pythons were smaller than those seen historically, while 21% felt that they had become bigger recently than those seen in the past. There were 25 respondents who did not answer this question.

4.4.4 Observations and experiences of pythons

Of the 438 respondents, 176 (40%) had encountered southern African pythons feeding. These observations included snakes that were actively eating, as well as those that had recently eaten, with the prey item clearly visible in their bellies. These included 31 identified animal species, including birds, mammals and reptiles (Table 4.5). There were also accounts of frogs and insects, as well as numerous non-specific reports of birds, antelopes, and rodents. Interesting feeding

observations and methods mentioned in the questionnaire included multiple references to pythons feeding on small birds at watering holes, waiting on branches near water for birds to perch close enough, feeding on weaver birds in nests, ambushing from under the surface at water holes and artificial water points, lying in wait on game trails and lying in wait under cut grass on roads.

Only 22% (n = 97) of the respondents had seen southern African pythons in burrows. Of these, 41 (42%) had seen pythons sheltering or retreating into burrows upon approach. The second-highest number of respondents' accounts (36%, n = 35) were related to pythons nesting with eggs visible in the burrows. Five pythons were seen to be digesting large meals; there were three accounts of snakes using the burrows for hunting; one account of hatchlings at a burrow mouth, and 12 respondents only reported that they had seen pythons in burrows.

Aardvarks (*Orycteropus afer*) were the species mentioned most often in relation to digging burrows for southern African pythons. Wild pigs (common warthogs (*Phacochoerus africanus*) and bushpigs (*Potamochoerus larvatus*)) were mentioned the second most frequently, and Cape porcupines (*Hystrix africaeaustralis*) were the third most frequently mentioned. Other options included termite (*Microhodotermes viator*) mounds, rabbit holes, cavities where roots had once been and erosion.

Respondents were also asked if they had ever encountered multiple southern African pythons at the same time, and 63 (14%) people responded with details. Of these, 13 sightings (21%) were of pythons observed basking, with one case detailing a female with two males (presumably identified by size, as the females attain much larger sizes). There were seven accounts of hatchlings being found together, with one account mentioning over 30 hatchlings and another account mentioning that the female was still present. There were six (10%) accounts of snakes being mobile together and one account of males fighting. Finally, there were 38 (60%) accounts

of pythons copulating, with one mentioning six males and one female, two accounts of three males and one female and one account of several males and one female.

Table 4.5: List of the prey species that respondents had identified pythons eating.

Common name	Scientific name	Wild / Domestic
Birds		
Domestic goose	<i>Anser anser domestica</i>	Domestic
Domestic chicken	<i>Gallus gallus domesticus</i>	Domestic
Hadedda ibis	<i>Bostrychia hagedash</i>	Wild
Lilac breasted roller	<i>Coracias caudatus</i>	Wild
Reed cormorant	<i>Microcarbo africanus</i>	Wild
Dark capped bulbul	<i>Pycnonotus tricolor</i>	Wild
Mammals		
Domestic cow	<i>Bos taurus</i>	Domestic
Domestic dog	<i>Canis lupus familiaris</i>	Domestic
Domestic goat	<i>Capra aegagrus hircus</i>	Domestic
Domestic guinea pig	<i>Cavia porcellus</i>	Domestic
Domestic cat	<i>Felis catus</i>	Domestic
	<i>Oryctolagus cuniculus</i>	
Domestic rabbit	<i>domesticus</i>	Domestic
Domestic sheep	<i>Ovis aries</i>	Domestic
Impala	<i>Aepyceros melampus</i>	Wild
Red duiker	<i>Cephalophus natalensis</i>	Wild
Samango monkey	<i>Cercopithecus mitis</i>	Wild
Vervet monkey	<i>Chlorocebus pygerythrus</i>	Wild
Giant rat	<i>Cricetomys ansorgei</i>	Wild
Waterbuck	<i>Kobus ellipsiprymnus</i>	Wild
Scrub hare	<i>Lepus saxatilis</i>	Wild
Tree squirrel	<i>Paraxerus cepapi</i>	Wild
Warthog	<i>Phacochoerus africanus</i>	Wild
Rock hyrax	<i>Procavia capensis</i>	Wild
Steenbok	<i>Raphicerus campestris</i>	Wild
Sharpe's grysbok	<i>Raphicerus sharpei</i>	Wild
Common reedbuck	<i>Redunca arundinum</i>	Wild
Common duiker	<i>Sylvicapra grimmia</i>	Wild
Greater cane rat	<i>Thryonomys swinderianus</i>	Wild
Nyala	<i>Tragelaphus angasii</i>	Wild
Bushbuck	<i>Tragelaphus sylvaticus</i>	Wild
Reptile		
Rock monitor	<i>Varanus albigularis</i>	Wild

In relation to the ecosystem services that southern African pythons provide and the perceived positive and negative impacts that pythons have on the cohabitant human populations, 13% (n = 56) were not aware of any positive impacts that pythons have, while 23% (n=101) were not aware of any negative impacts. Significantly more participants were not aware of the negative impacts than those who were unaware of the positive impacts ($\chi^2 = 15.024$, df = 1, $p < 0.001$). By analysing the responses to certain of the questions, we could deduce that 54% (n = 235) of the respondents had not seen pythons in real life before, meaning that less than half of the individuals responding had encountered live, wild pythons.

4.5 Discussion

The results were not as predicted, with a significant majority having an overall positive attitude towards southern African pythons. Valuable insights into the cultural significance of these pythons and how this trend is evolving over time were obtained, as well as some insight into the misinformation surrounding this species and the factors that influence these perceptions.

4.5.1 Attitudes, feelings, and perceptions of pythons

While preparing this study, it became clear that there is a severe lack of recorded information regarding perceptions and attitudes towards snakes, specifically in Africa. This dearth of information makes it impossible to predict people's responses, reactions or sensitivities to snakes, which is an important consideration in environmental education initiatives as well as the conservation and management of species and areas [17, 20, 24, 25]. This becomes particularly relevant when Tolley et al.'s [15] concerns for the species are considered, which include the impact of traditional medicine and harvesting for markets, etc.

The overall positive attitude towards southern African pythons was encouraging, and the diversity of reasons behind this positive attitude was intriguing (Fig. 4.1). This data confirmed what has been mentioned in literature [3, 9, 10, 28], that southern African pythons hold an important and multi-faceted place in African society; it would be valuable to try to understand the intricacies of this relationship further in order to understand and document pythons' cultural significance as well as to be aware of threats we may not otherwise be cognisant of, and thus be able to put suitable mitigating measures or protection in place. There appears to be an overall reluctance to kill pythons for cultural, environmental, or simply fear-related reasons (Fig. 4.3). However, there were several extremely negative responses, for example, where people mentioned “hating” them and associated them with evil. A surprisingly large proportion of the population believed they were dangerous to humans, while fewer thought they would eat people. This fear is understandable because of their size and extremely generalist feeding behaviours; however, to date, there are no authenticated published records of southern African pythons feeding on human beings [30]. There was, however, a documented case of a boy being killed by a python [23]. Given that pythons are such generalist and efficient predators, it seems likely that suitably sized humans would be considered prey by large pythons. However, considering their abundance in close proximity to human habitations for centuries, it is surprising that there are not more authenticated accounts. Pythons are intelligent and efficient predators; humans may be too “high-risk” as prey items to feature routinely.

There were several rumours (various pers. comm.) that the questionnaire attempted to investigate. One of which was that, because of changes in society, pythons are no longer afforded the traditional protection they once enjoyed, largely because younger people lack exposure to and appreciation of traditional stories and beliefs. This did not appear to be the case, and in fact, the

opposite seemed to be true. The younger people seem to be more educated and thus less fearful of pythons. This is a phenomenon that might be reflected throughout the world as traditions and customs hold less and less sway over societies [31] and should be borne in mind with similar studies and in situations where “traditions and cultures” are used as means of protecting environments or species – a popular concept in underdeveloped countries [32, 33].

This finding, however, contradicted the results of the binary regression model, which showed that older people were much more likely to react positively to the southern African pythons. There are several possible explanations for this. Firstly, it is likely that the more traditional, older respondents would be more likely to retain some culturally positive feelings towards pythons, as the majority of respondents who expressed their cultural feelings towards pythons reported positive views. There is also the concept that older people are more knowledgeable and have more experience, which would lead to a more informed attitude towards pythons, suggesting a more positive outlook. Younger people would also be more exposed to media and universal concepts, such as this innate fear of snakes [2]; however, they should also be more educated about harmless snakes and the ecosystem services that snakes provide. Unemployed people are likely to be less educated; however, they are also more likely to be in a negative mental state due to unemployment, and therefore, are more likely to be more negative towards anything [34]. Unemployed people would also feel the loss of livestock more as they have less financial buffering to purchase new stock.

The attitudes of people outside of KwaZulu-Natal being more favourable about southern African pythons than those inside is hard to explain; it could be cultural, where the people groups within the KwaZulu-Natal borders are less favourable towards pythons than the groups outside, or it could be that those who are within KwaZulu-Natal have more exposure to pythons than those

outside, as most of KwaZulu-Natal falls within their range distribution. This, however, contradicts the final predictor, which was that those who had encountered pythons were more likely to have a positive attitude. This finding was reflected by a similar study in Brazil [35]. This is further evidence that public exposure to environments and species is essential to conservation and that people are more likely to engage with, like and even protect what they are familiar with or have encountered [11] – valuable insights for conservation initiatives.

From the data, it was apparent that rural people were more negative towards southern African pythons than urban people. This could be explained by urban-dwelling people not being exposed to the negative impacts of pythons, such as their livestock being taken by pythons. We also found that a higher percentage of people with isiZulu as their home language were negative towards pythons than those who had English as their home language. However, it was encouraging to note that a fair percentage (23%) of isiZulu home language speaking people had a positive attitude towards these snakes.

We found that the respondents' level of education and gender, regardless of whether they lived in rural or urban settings, did not affect their attitudes toward southern African pythons. This can be attributed to the large-scale migration of people from rural areas to urban areas, resulting in a less distinct divide between rural and urban populations. Technology and exposure to social media may also contribute to this lack of differences. These results were interesting as there is a general idea that women are more fearful of snakes than men [12, 35]; however, this was not the case. This is possibly because of boys and girls being exposed to the same cultural beliefs and narratives surrounding these snakes. It was also assumed that those with a tertiary level of education would be less fearful than less educated people [35], however, this was also not the case,

possibly due to fear being an intrinsic part of the human psyche, not influenced by education, proving that generalisations and pre-conceived ideas are dangerous.

4.5.2 Observations and experiences of pythons

The answers to the observation and experience questions were insightful; the level of detail and interest that some respondents provided demonstrated a genuine fascination and interest in the species, as evidenced by the positive responses. While it is recognised that citizen science in the form of questionnaires has its limitations concerning the validation of specific observations and accounts [36], trends did appear. For example, the use of aardvark holes, the use of burrows for nesting and digesting, multiple males involved in mating behaviours (with one account of six males and one female and several accounts of three males), as well as feeding behaviours, including taking birds from branches and animals from water sources, including troughs. In relation to the species that respondents had observed being preyed upon, the answers were challenging, with many vague references to rodents, antelope and birds. Of the species that were specifically identified, all except one (reed cormorant, *Microcarbo africanus*) were species already known to form part of the pythons' diet (Table 4.5) [30]. These comments provide useful supporting information for observations made elsewhere.

Concerning the ecosystem services that southern African pythons provide and the perceived positive and negative impacts that pythons have on the cohabitant human populations, significantly more participants were not aware of negative impacts than those who were unaware of positive impacts, implying that the general population is more aware of the ecosystem services that pythons specifically provide than the negative impacts that they have, which is a positive finding for conservation measures. The ecosystem services that pythons provide are an aspect that

should be stressed in environmental education initiatives, as there are important direct (e.g., pest control [37]) and indirect (e.g., tourism [38]) benefits that local human populations could receive from these, presently persecuted, predators.

While this study by no means defines people's attitudes and perceptions towards southern African pythons, it does shed light and lend a scale to many of the myths and theories surrounding these evocative reptiles. It is encouraging that the overall attitude towards them was significantly positive; it was also encouraging that, theoretically, people would be less inclined to kill them than to remove them. It is positive that most people recognised the benefits that pythons provide. However, these data also revealed a concerning amount of misinformation about pythons as well as exploitation and persecution of the species for various uses, including meat, *muthi* and protecting assets. There was an overriding trend of interest in this species, which could be leveraged by education and information sharing, towards the conservation of this important snake species and its habitat.

4.5.3 Limitations

Regarding the limitations of questionnaires, it is worth considering precisely what questions you want to ask and why. The language barrier is a serious obstacle, even when the questionnaire is translated accurately; the exact meaning of your question can be missed in the translation. For example, some of the questions about *muthi* use, cultural beliefs and superstitions were inconclusive. Where we had assumed that all the *muthi* uses would have been listed in answer to that question, it was only in interpreting the answers to all three questions that the most thorough understanding could be achieved. As such, it is extremely important to consider this when designing questionnaires and even when interpreting the results. Another example related to which

age group was more scared of snakes. This question was included because there was an assumption that older generations were more likely to be fearful and respectful of them from a cultural perspective, while younger generations would not be as bound by these norms. However, it became obvious from the answers that this was not how the question was understood. Rather, they were answering from the point of view that children are naïve and perhaps the older generations are less educated and not as knowledgeable about pythons.

4.5.4 Conclusions

A surprisingly positive attitude towards the southern African pythons was revealed, despite awareness of the negative impacts of pythons, such as livestock raiding. There was an array of positive opinions towards these predators, ranging from beautiful and meaningful for tourism to important for their pest control and the place they hold in the food chain, as well as for their uses in *muthi*. The positive attitude towards pythons was most heavily influenced by age and previous exposure to pythons. Most thought that they were harmless to humans, but 10% thought they were deadly, suggesting that most of the population does not fear for their lives from these snakes. Pythons still hold an important place culturally and traditionally, with a percentage (22%) of the population, and it is unclear if this prevalence is less than in the past. We did not discover any valuable breeding or behavioural information; however, we found evidence of multiple males being involved in breeding events, substantial burrow usage, primarily using aardvark burrows, and that only just over half of the respondents had actually encountered pythons in the wild.

From the literature and the results of this research, it becomes even clearer how important education, as well as experiences and encounters with these animals, are for conservation and species preservation. With a large species like the southern African python, their breeding and

behavioural ecology seem stacked against them in the modern world. They have a slow and extremely energy-intensive reproductive mode, they only reach sexual maturity at a large size, and are particularly vulnerable once big [39]. They are also renowned for their negative impact on human settlements and, paired with this, are easy to track, locate and kill, leaving pythons susceptible to human exploitation and even extermination [14, 15].

In response to the insights gained from this study, a poster has been created to address several myths and incorrect beliefs surrounding southern African pythons (Supplementary information Figure S4.1). This poster has been translated, featuring English and isiZulu facts side by side on the same document, creating a language aid as well as a biological science tool, thereby rendering it more valuable to educational institutions. It will be distributed as widely as possible, especially to schools, within the southern African python's distribution range, to address some of the misinformation about this species.

4.6 Acknowledgements

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4.8 Supplementary information

Supplementary information S4.1. Questionnaire used in the present study.

Python Perceptions and Persistence Questionnaire

Thank you for taking the time to fill in this questionnaire. It forms part of the research involved in a PhD project presently being undertaken at the University of Kwa-Zulu Natal, Pietermaritzburg.

Pythons are a large, obvious species of snake that have both a positive and a negative impact on their human neighbours.

Being large snakes, they frequently predate on livestock, which has financial implications for the stock owners, however they also have a positive impact by consuming a large number of pest species that could have a considerably greater negative impact than the snakes themselves. They also have both positive and negative spiritual and social connotations. As such their population and distribution is impacted by the attitude of the communities towards this species. This aspect of the study aims to establish the nature of the relationship between the community in the area and this snake species as well as whether numbers are increasing or decreasing. Other anecdotal information that can be gathered about the snake will also be documented and used in the final write up.

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This questionnaire has been approved by the Humanities and Social Sciences Research Ethics Committee. Reference Number: HSSREC/00006162/2023

CONSENT TO PARTICIPATE IN THE STUDY

Participation in this study is anonymous, and therefore, no identity shall be revealed.

I have been informed about the study entitled “Movement, burrow use, social interactions and persistence of southern African pythons (*Python natalensis*) in KwaZulu-Natal, South Africa” I understand the purpose and procedures of the study. I have been given an opportunity to answer questions about the study that have been asked to my satisfaction. I declare that my participation in this study is entirely voluntary and that I may withdraw at any time. If I have any further questions/concerns or queries related to the study, I understand that I may contact the researcher. If I have any questions or concerns about my rights as a study participant, or if I am concerned about an aspect of the study or the researchers then I may contact Prof Downs of the University of KwaZulu-Natal.

1. Do you consent to the above information? *

Yes, No

Demographics

2. Gender

Male, Female, Prefer not to say

3. How old are you?

18-25 years, 26-33 years, 34-41 years, 42-49 years, 50+ years

4. Level of education

None, Primary School, Secondary School, Tertiary Education (University)

5. Where do you live?

In a town, In a city, Rurally

6. What is your home language

English, IsiZulu, Afrikaans, Xhosa, Tswana, Sesotho, Venda, Sepedi

7. Employment

Employed, Unemployed

8. What province are you from?

Kwazulu-Natal, Mpumalanga, Eastern Cape, Western Cape, Gauteng, North West, Free State, Northern Cape, Limpopo, Outside SA

9. If outside SA, which country?

10. How long have you worked or lived in this area?

0-5 years, 6-10 years, 11-15 years, 16-20 years, 20+ years

Pythons – in relation to people

11. On a scale of positive to negative, how do you view pythons?

(With 1 being purely positive, 2 being mostly positive but aware of some negatives, 3 being neutral or undecided, 4 being negative but aware of some positives and 5 being purely negative.)

1 2 3 4 5

12. Briefly, what are your feelings, thoughts and beliefs about Southern African Pythons? Why?

13. Why do you view them this way?

14. What positive impacts are you aware of pythons having on the environment and on humans?

15. What negative impacts are you aware of pythons having on the environment and on humans?

16. What cultural significance do pythons have in your community?

17. Are you aware of any traditional medicine uses for pythons?

18. Are you aware of any superstitions specifically involving pythons?

19. On a scale, how would you respond to encountering a python near your homestead?

(With 1 being kill it immediately, 2 being chase it away but not necessarily kill it, 3 being ignore it completely and 4 being encourage it to be there.)

1 2 3 4

20. Is there a difference in the way different age groups respond to pythons?

21. On a scale, how confidently can you identify a python compared to another snake?

(With 1 being absolutely certain you know exactly what a python looks like, 2 being you're pretty sure you know what it looks like, 3 not really confident and 4 being not confident at all, they all look the same.)

1 2 3 4

22. How dangerous to humans do you think pythons are?

(With 1 being absolutely deadly, one bite will kill me, 2 being they are very dangerous, I'll get very sick but I won't die, 3 being I will get sick but will recover and 4 being they are harmless to humans.)

1 2 3 4

23. Do you think pythons eat humans?

(With 1 being definitely yes, 2 being you think they could or have heard about it happening, 3 being you doubt it and 4 being you know they don't.)

1 2 3 4

Pythons - Distribution and population

24. On a scale of increasing to decreasing, how often do you encounter pythons compared to in the past?

(With 1 being a lot more often than in the past, 2 being slightly more often than in the past, 3 being the same amount as before, 4 being slightly less often than in the past and 5 being definitely a lot less often than in the past.)

1 2 3 4 5

25. On a scale of larger to smaller, what size are the pythons you've encountered recently compared to those encountered historically?

(With 1 being the recently encountered snakes are considerably larger, 2 being the recently encountered snakes are a bit larger, 3 being you're not sure or they are not noticeably larger, 4 being they are a bit smaller than historically, and 5 being they are a lot smaller than historically.)

1 2 3 4 5

Pythons - Burrow use and breeding/social behaviour

26. Have you observed pythons in burrows? What were they doing in the burrow?

27. Have you observed python nests? Where were they?

28. Have you encountered more than one python in a single site? What were they doing?

29. Of the burrows encountered, what do you think originally dug the burrow?

Pythons - Diet

30. Have you encountered feeding pythons? What were they feeding on and what size where the snakes?

31. Have you observed any specific hunting or ambushing behaviour in pythons?

32. Do you have any interesting observations or stories about pythons?

33. Do you have any questions or things you would like to say?

Thank you!

Supplementary information S4.2 Consent form used in the present study

UKZN HUMANITIES AND SOCIAL SCIENCES RESEARCH ETHICS COMMITTEE (HSSREC)

Information Sheet and Consent to Participate in Research

Date: 12 July 2023

STUDY: Movement, burrow use, social interactions and persistence of southern African pythons (*Python natalensis*) in KwaZulu-Natal, South Africa

RESEARCHER DETAILS: Ms Kirsty Kyle (PhD candidate), Email: [REDACTED]; Prof. Colleen T. Downs (Supervisor), Email: downs@ukzn.ac.za

STUDY DESCRIPTION

Pythons are a large, obvious species of snake that have both a positive and a negative impact on their human neighbours. Being large snakes, they frequently predate on livestock, which has financial implications for the stock owners, however, they also have a positive impact by consuming a large number of pest species that could have a considerably greater negative impact than the snakes themselves. They also have both positive and negative spiritual and social connotations. As such, their population and range distribution are impacted by the communities' attitudes towards this species. This aspect of the study aims to establish the nature of the relationship between the community in the area and this snake species as well as whether numbers are increasing or decreasing. Other anecdotal information that can be gathered about the snake will also be documented and used in the final write up of the thesis.

CONSENT TO PARTICIPATE IN THE STUDY

Participation in this study is anonymous, and therefore, no identity shall be revealed.

I have been informed about the study entitled “Movement, burrow use, social interactions and persistence of southern African pythons (*Python natalensis*) in KwaZulu-Natal, South Africa”. I understand the purpose and procedures of the study. I have been given an opportunity to answer questions about the study that have been asked to my satisfaction. I declare that my participation in this study is entirely voluntary and that I may withdraw at any time. If I have any further questions/concerns or queries related to the study, I understand that I may contact the researcher at [REDACTED].

If I have any questions or concerns about my rights as a study participant, or if I am concerned about an aspect of the study or the researchers, then I may contact Prof Downs of the University of KwaZulu-Natal, Pietermaritzburg campus (Cell no. [REDACTED] [REDACTED], Email: downs@ukzn.ac.za).

This study has been ethically reviewed and approved by the UKZN Humanities and Social Sciences Research Ethics Committee (approval number HSSREC/00006162/2023).

In the event of any problems or concerns/questions, you may contact the researcher at (provide contact details) or the UKZN Humanities & Social Sciences Research Ethics Committee; contact details as follows:

HUMANITIES & SOCIAL SCIENCES RESEARCH ETHICS ADMINISTRATION

Research Office, Westville Campus

Govan Mbeki Building

Private

Bag

X

54001

Durban

4000

KwaZulu-Natal, SOUTH AFRICA

Tel: 27 31 2604557- Fax: 27 31 2604609

Email: HSSREC@ukzn.ac.za

CONSENT

I(Name) have been informed about the study entitled Movement, burrow use, social interactions and persistence of southern African pythons (*Python natalensis*) in KwaZulu-Natal, South Africa by Ms Kirsty Kyle (PhD candidate).

I understand the purpose of the study.

I have been given an opportunity to answer questions about the study and have had answers to my satisfaction.

I declare that my participation in this study is entirely voluntary and that I may withdraw at any time.

If I have any further questions/concerns or queries related to the study, I understand that I may contact the researcher at (provide details).

If I have any questions or concerns about my rights as a study participant, or if I am concerned about an aspect of the study or the researchers, then I may contact:

Ms Kirsty Kyle (PhD candidate), Email: [REDACTED]; Cell: [REDACTED]
Prof Colleen T. Downs (Supervisor), Email: downs@ukzn.ac.za; Tel: 033: 2605127; Cell: [REDACTED]

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Signature of Participant

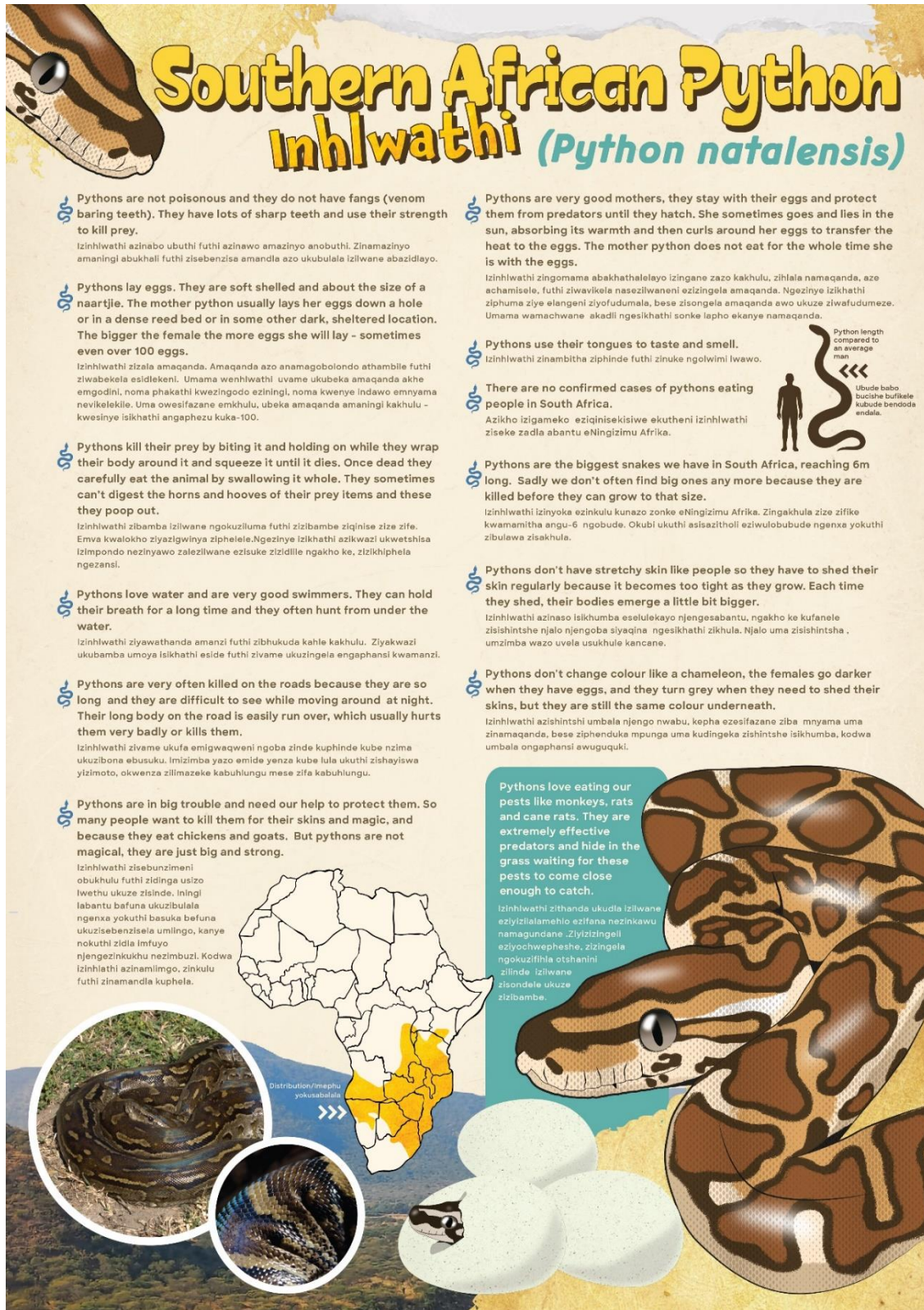
Date

**Signature of Witness
(Where applicable)**

Date

**Signature of Translator
(Where applicable)**

Date



Supplementary information Figure S4.1. Infographic poster about pythons which replaces myths with facts about this species.

CHAPTER 5

Protected and yet pressured: Persistence of southern African pythons (*Python natalensis*) in South Africa despite changing land use and other anthropogenic threats

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Running header: Python persistence

5.1 Abstract

Around the globe, changing landscapes and habitat transformation are major factors affecting wildlife. In recent years, South Africa has experienced significant population growth and migration, leading to the transformation and expansion of both rural and urban areas, with the loss of natural areas. We used locality records to determine whether southern African pythons (*Python natalensis*) persist despite ongoing land transformation in South Africa, assess the threats they face, and identify vegetation types in which they occur. We retrieved locality records of southern African pythons from literature, institutions, and citizen science sources, both before and after 2015, to determine occurrence, and we used geographic information system software to map their distribution. Pythons showed a preference for the forest biome, followed by the Indian Ocean Coastal belt, with slightly more records from protected areas than from non-protected areas. We substantiated anthropogenic threats, including road mortality, electric fencing, and fires. We documented 15 species of animals feeding on pythons, as well as three species that killed them without consuming them. Considering the important ecological niche that these snakes fill, as both predators and prey, it is vital that they receive as much protection as can be afforded to them. We suggest mitigation strategies for some of the anthropogenic threats southern African pythons face.

Keywords: habitat transformation, trophic niche, reptile, environmental change, predation

5.2 Introduction

Land use change is considered one of the most significant drivers of the decline in landscape stability (Prokopová et al. 2019) and is recognised worldwide as the greatest threat to biodiversity, having caused declines in the health, diversity, and populations of species and ecosystems (Davison et al. 2021). Land use change is defined as human-induced modification of Earth's terrestrial surfaces (Ellis 2013) and encompasses transformations from natural to agricultural land and/or to urban areas. Agricultural transformation is known to have numerous negative environmental impacts, including desertification, soil erosion, overexploitation of natural resources, and decreased ecological resilience (Kosmas et al. 2016). In recent years, South Africa has experienced significant population growth and migration, leading to the transformation and expansion of both rural and urban areas, with the loss of natural areas (Jewitt et al. 2015). KwaZulu-Natal, although largely considered rural, is characterised by a high housing density with many peri-urban areas (Khowa et al. 2023).

Urbanisation is generally considered a global threat to biodiversity (Theodorou 2022), with the most common response being a shift from specialist to generalist species (Concepcion et al. 2015). Some species thrive in this transformed habitat; however, the biodiversity and ecological richness are typically markedly reduced by this extreme form of land transformation (Downs et al. 2021). The complex relationship between biodiversity and land use is highly context-dependent (Haines-Young 2009). There is some evidence that snakes (particularly pythons) can persist with urbanisation and even thrive in areas of changing land-use (Shine et al. 1999; Fearn et al. 2001). Africa is known to be underrepresented in this research (Downs et al. 2021), specifically in relation to reptiles (Tolley et al. 2023; Genevier et al. 2025).

A large amount of recent anthropogenic land-use transformation, with known detrimental effects on the environment, is characterised by urban sprawl (Nuissl and Siedentop 2021). African and Asian cities are the fastest-growing urban environments in the world, with Africa predicted to take the lead between 2025 and 2050 (Kundu and Pandey 2020). These ever-increasing levels of urbanisation pose multiple challenges, including food security and housing (Kundu and Pandey 2020). South Africa has experienced an increase in its human population, accompanied by large-scale and persistent urban migration, resulting in increased pressure on urban areas and a corresponding expansion in their size (Mthiyane et al. 2022). A lack of planning and provision for the expanding urban populations has had a strongly negative impact on natural amenities and resources, including water and sanitation, resulting in negative environmental impacts (Boadi et al. 2005).

Southern African pythons (*Python natalensis*) are a contentious species because of their potential to reach large sizes, their propensity for living in close proximity to human habitation, and their generalist diet, specifically the wide variety of domestic species which are included (Branch 1998; Dube and Kavhu 2022; Kyle and Downs 2025). While presently categorised “Least Concern” in the IUCN Red List since 2019, many southern African python populations are known to be declining, with some local extinctions in the Eastern Cape and KwaZulu-Natal provinces, while in other areas they appear to be expanding their range (Alexander and Tolley 2021). Their large body size makes these snakes particularly vulnerable to anthropogenic threats, including electrocution by fences, vehicle strikes on roads and wanton killing because of the perceived threat to livestock, as well as harvesting for food, traditional medicine (*muthi*), fashion and the pet trade (Broadley 1983; Branch 1998; Tolley et al. 2023; Cormac et al. 2025).

Due to the dire situation posed by land-use change in South Africa, combined with the multiple anthropogenic threats southern African pythons face, it is essential to establish and document their persistence across natural, rural, peri-urban, and urban environments. Knowing their preferred vegetation types also enables better protection of this species and its habitats. We compared the locality data for southern African pythons in South Africa before and after 2015 to determine whether there were any noticeable differences over time. This resulted in the following objectives:

1. To establish if southern African python populations were persisting despite the land use change in many areas.
2. To establish which vegetation types they preferred.
3. To establish if there was a reliance on protected areas for their persistence.
4. To assess the threats they face, particularly in relation to their close proximity to humans.
5. To suggest possible mitigating methods that could be applied to protect these snakes.

We hypothesised that, while some southern African pythons can persist in urban and agricultural areas, their large body size and later maturation age make them particularly vulnerable to anthropogenic threats, and their ongoing persistence in these areas will require efforts to protect them.

5.3 Methods

Records of southern African python localities were retrieved from as many sources as possible, including iNaturalist®, the Global Biodiversity Information Facility (GBIF), the Port Elizabeth Museum, the Transvaal Museum, the University of Cape Town's Animal Demography Unit, the South African National Biodiversity Institute (SANBI), and the Ezemvelo KZN Wildlife database.

These records were collected through to July 2025 and compiled into an Excel® spreadsheet, yielding 3,085 southern African python locality records. These data were cleaned, with duplicates and records lacking global positioning system (GPS) location coordinates removed, resulting in a dataset of 866 southern African python occurrence records.

We then retrieved southern African python sightings from citizen science sources, with a particular focus on Facebook® pages and WhatsApp® reptile groups. Only sightings with suitable information were recorded, including a date and a locality accurate to within ~20 km. Photographic evidence was a requirement on the Facebook® posts, as people often misidentify snakes (Wolfe et al. 2020). Other python occurrence records were retrieved from reliable sources or from authors who either work with reptiles frequently (e.g., snake catchers) or are in the wildlife profession (e.g., conservation management or tourism). This added 371 additional records of southern African python occurrences to the dataset.

We then sorted the data to separate the southern African python occurrence records into two groups: those before and after 2015. A concerted effort was made to gather records for the 2014 Reptile Red Data book, and, as a result, we chose 2015 as the pivotal date, with data from 2015 included in the “post” category. As the second Reptile Red data book was produced in 2023, following a second push for occurrence data, by 2025, we had obtained a suitable ten-year gap.

We then used QGIS (Version 3.38.1 - Grenoble) to create the southern African python occurrence distribution maps with quarter-degree grid squares, comparable to those of the South African Reptile Conservation Assessment (SARCA) project. These maps show the number of localities per grid square according to the colour code described in the legend. A map was then created showing the number of grid squares that contained sightings before 2015, after 2015, and in both periods. This was done to address observer bias in areas where there are likely to be more

sightings, for example, within nature reserves. We also overlaid vegetation (South African National Biodiversity Institute 2025) and protected areas' (Department of Forestry, Fisheries and Environment 2025) shapefiles and extracted the number of grid squares that fell within the different vegetation types, as well as those that fell within various types of protected areas. With the sightings and vegetation type data, we assessed whether the distribution of the sightings across the vegetation types was proportional to the availability of each habitat type by comparing the observed counts of sightings against expected counts derived from the relative area (km²) of each vegetation type within the study area. A chi-square goodness-of-fit test was conducted in R, and the expected probabilities were calculated as the proportion of the total study area occupied by each vegetation type. Standardised residuals were then examined to identify which categories contributed most strongly to deviations from the expected (R Core Team 2023).

A point file containing all southern African python occurrence records for South Africa was created in ArcGIS Pro v3.6.1 (ESRI, 2025). The area (km²) covered by each biome (Vegmap, South African National Biodiversity Institute, 2026) in the recorded python occurrence region was determined using the Clip tool to create a custom extent and calculated using the Calculate Geometry tool (ESRI, 2025). We collected elevation data (SRTM 30, South African Department of Science and Technology, 2018) using the Add Surface Information tool (ESRI, 2025), employing a bilinear method with a 5 m search distance. We added vegetation, biome and bioregion data (Vegmap, South African National Biodiversity Institute, 2026) using the Spatial Join tool (ESRI, 2025) with a 5 m search radius. A custom quarter-degree grid cell layer was created for the total area of recorded python occurrences, with average elevation and predominant vegetation, biome, and bioregion data added to each cell using the same tools as above.

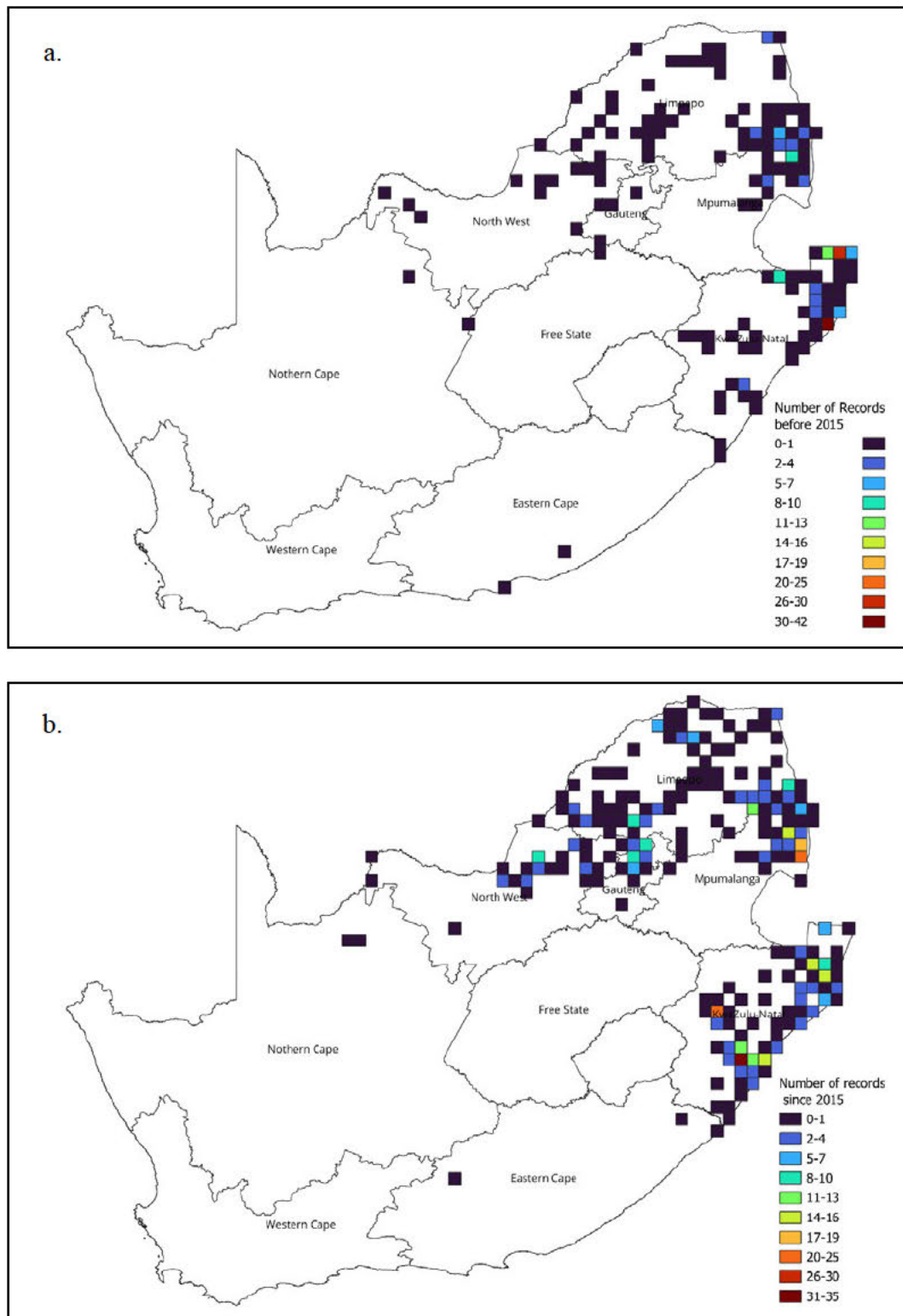
To gather data on southern African python predation and mortality, we used the same Facebook® search and WhatsApp® groups, as the search for “pythons” revealed both localities and predation and fatality events. We searched iNaturalist® for “research grade” southern African python records and manually sorted them, checking for clear roadkill photographs or records that were listed as “road kill” or “dead on road”. We also utilised data from the Endangered Wildlife Trust’s Annual Report on reducing impacts on wildlife and enhancing motorist safety on three major toll routes in South Africa (Leeuwner and Hlatshwayo 2025). We incorporated data from a roadkill study conducted within the Isimangaliso and Hluhluwe-Imfolozi parks (Cormac et al. 2025). Finally, we utilised records gathered from social media for a study examining the diets of southern African pythons (Kyle and Downs 2025), as this information was also relevant to the present study.

5.4 Results

5.4.1 Southern African python occurrence

In total, we obtained 1,237 records of southern African python occurrence in South Africa for the period 1907 to 2025. Most of these were obtained from historical and open-source datasets ($n = 911$, 74%), while the remainder ($n = 326$, 26%) were obtained from social media, personal communications and personal records. There were significantly different numbers of southern African python occurrence records for the two time periods ($\chi^2 = 112.47$, $df = 1$, $p\text{-value} < 0.05$), with almost double the number of records after 2015 compared with before (432 before 2015 and 805 subsequently). Although survey effort increased post 2015, the overall range of the species did not change much; however, there was an increase in the number of known localities within the range. This translated into 53 quarter-degree grid cells with sightings from before 2015, 88 grid

cells with sightings from both time periods and 119 grid cells with sightings from afterwards (Figure 5.1).



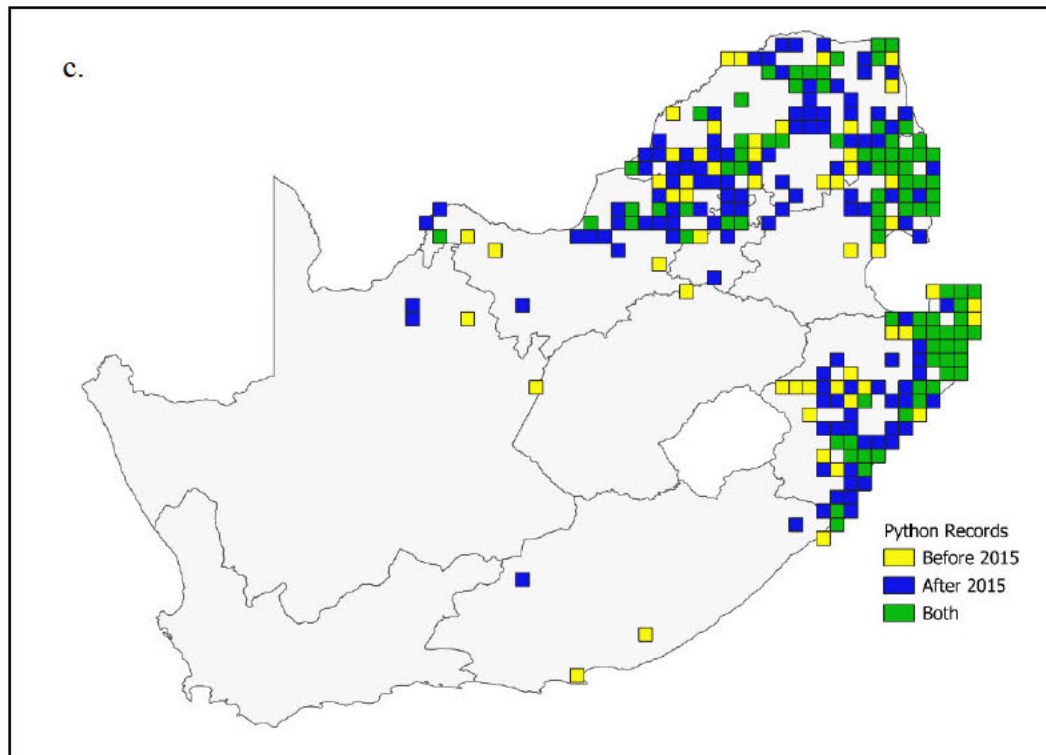


Figure 5.1: Maps showing the distribution of the southern African python (*Python natalensis*) occurrence records from before (a.) and after (b.) 2015, and c. shows the distribution of grid cells containing records before 2015 in yellow, after 2015 in blue, and both in green.

5.4.2 Environmental parameters

3.2.1 Vegetation

Plotting the pythons' occurrence localities onto the 2024 Vegetation map of South Africa (South African National Biodiversity Institute 2025) indicated a highly significant departure from proportional use of vegetation types ($\chi^2 = 1476.9$, $df = 7$, $p < 0.0001$, Table 5.1). Standardised residuals revealed that sightings were substantially higher than expected in Forests (+32.1), Indian Ocean Coastal Belt (+13.4), and Savanna (+4.7), with a smaller positive deviation in Azonal Vegetation (+2.1). In contrast, Grassland (−14.3), Albany Thicket (−5.4), and Nama-Karoo (−2.6)

had markedly fewer sightings than expected given their area. Fynbos showed no meaningful deviation (residual ≈ 0.6).

Table 5.1: Number of southern African pythons, *Python natalensis*, recorded in the different vegetation biomes of South Africa (South African National Biodiversity Institute 2025) in the present study.

Biome	Area of each vegetation type within the snake records polygon (km ²)	No. of records	Percentage of records	Percentage of total vegetation type within the polygon
Albany Thicket	12925.4	1	0.1	2.6
Azonal				
Vegetation	3918.9	16	1.3	0.8
Forests	3715.1	105	8.8	0.7
Fynbos	549.6	2	0.2	0.1
Grassland	144132.1	81	6.8	29.0
Indian Ocean				
Coastal Belt	11691.1	99	8.3	2.4
Nama-Karoo	3610.0	1	0.1	0.7
Savanna	315852.9	890	74.5	63.6

Within the Forest Biome, the most records of southern African pythons were found in the Northern Coastal Forest, followed by Sand Forest. In the Indian Ocean Coastal Belt, the most pythons were recorded in the Maputaland Coastal Belt, followed by the KwaZulu-Natal Coastal Belt Grasslands, and finally in the Savanna, the most records came from the Granite Lowveld, followed by the Zululand Lowveld (Table 5.2).

A comparison of the results from the two different methods used in the vegetation data analyses is shown in Appendix 5.1. The results showed that for finer-scale habitat work, grid cells were not always the most accurate method. According to the grid method, no southern African

pythons were found in the Indian Ocean Coastal Belt, whereas the sightings method recorded the second-highest occurrence there.

Table 5.2: The four vegetation types within the top three biomes that contained the highest number of southern African python sightings.

Forests	No. records
Northern Coastal Forest	43
Sand Forest	40
Lowveld Riverine Forest	12
Scarp Forest	5
Indian Ocean Coastal Belt	
Maputaland Coastal Belt	43
KwaZulu-Natal Coastal Belt Grassland	41
Maputaland Wooded Grassland	6
Pondoland-Ugu Sandstone Coastal Sourveld	6
Savanna	
Granite Lowveld	142
Zululand Lowveld	62
Central Sandy Bushveld	59
Tshokwane-Hlane Basalt Lowveld	59

3.2.2 Elevation

For the southern African python elevation data, the average elevation for each grid cell was calculated and binned into 200 m groupings. The number of grid cells within each bin was then counted throughout the convex hull polygon that included all of the python records and the total number of grid cells was compared to those that contained python records. From this, it was apparent that the highest percentage of occupation was in the lower-elevation areas, particularly the lowest, with 81% of the possible grid cells below 200 m a.s.l. containing records (Table 5.3).

Table 5.3: The distribution of southern African python records according to the mean elevation of the grid cells they were recorded in.

Elevation range (m a.s.l.)	Available	Occupied	Percentage occupied (%)
1-200	59	48	81
201-400	75	22	29
401-600	62	23	37
601-800	50	18	36
801-1000	97	31	32
1001-1200	186	50	27
1201-1400	187	46	25
1401-1600	111	17	15
1601-1800	22	2	9
1800-2500	7		0

5.4.3 Conservation status

Of the 1,237 southern African python total occurrence records, 661 (53%) were from within the boundaries of protected areas, either national parks, private nature reserves or conservancies (Table 5.4). Within those protected areas, 509 (77%) records were from government/national parks, 106 (16%) from private nature reserves, and 46 (7%) from conservancies. A binomial test revealed that python records were significantly overrepresented in protected areas compared with the national coverage (661 out of 1237 records; 53.4% observed vs. 9.2% expected; $p < 0.001$).

Table 5.4: Distribution of southern African pythons (*Python natalensis*) occurrence records within protected and non-protected areas in the present study.

	Protected area	Non-protected area	Total
Before 2015	314	118	432
Since 2015	347	458	805
Total	661	579	1 237

5.4.4 Threats

5.4.4.1 Anthropogenic threats

iNaturalist® revealed 30 incidents of southern African pythons killed on the roads between 2013 and 2025. These incidents spanned five southern African countries and five provinces within South Africa. A further 61 individuals were recorded as roadkill events in the Endangered Wildlife Trust Traffic Report (Leeuwner and Hlatshwayo 2025), as well as nine python roadkills reported during a roadkill survey project in Isimangaliso Wetland Park over three years (Cormac et al. 2025). Evidence of two southern African pythons killed by electric fences was found; however, several accounts of southern African pythons “rescued” from electric fences appeared in popular articles, and numerous anecdotal accounts described electric fences as a serious problem for large-bodied southern African pythons, especially after they had swallowed large prey. Another threat that southern African pythons face, exacerbated by human activities, was fire. Through literature searches and personal communications, we found evidence of four southern African pythons killed by fires, including one from a wildfire and three from management burns, with two pythons found together in a single management fire incident.

5.4.4.2 Natural threats

From data gathered across various sources, 15 species of birds, mammals, and reptiles were recorded feeding on southern African pythons, ranging from hatchlings to adult specimens (Table 5.5). Three mammalian species, African elephants (*Loxodonta africana*), Chacma baboons (*Papio ursinus*) and banded mongooses (*Mungus mungo*), were recorded killing southern African pythons without eating them on multiple occasions. There were also several anecdotal accounts of leopards (*Panthera pardus*) killing, but not eating, pythons. Five accounts of southern African pythons

being found dead, having been impaled internally by the sharp parts of swallowed prey items, were found on social media. Two accounts were of porcupine quills, one was a common duiker (*Sylvicapra grimmia*), one was a young male impala (*Aepyceros melampus*), and one was a blue duiker (*Philantomba monticola*).

Table 5.5: Species recorded killing southern African pythons (*Python natalensis*) from social media records and literature.

Species	Scientific name	Eaten	Killed	Taxon
Crowned eagle	<i>Stephanoaetus coronatus</i>	1		Bird
Marabou stork	<i>Leptoptilos crumenifer</i>	1		Bird
Saddle-billed Stork	<i>Ephippiorhynchus senegalensis</i>	2		Bird
Brown hyena	<i>Parahyaena brunnea</i>	1		Mammal
Spotted hyena	<i>Crocuta crocuta</i>	1		Mammal
Honey badger	<i>Mellivora capensis</i>	4		Mammal
Leopard	<i>Panthera pardus</i>	5		Mammal
African lion	<i>Panthera leo</i>	1		Mammal
Large spotted genet	<i>Genetta tigrina</i>	1		Mammal
Banded mongoose	<i>Mungos mungo</i>		3	Mammal
African elephant	<i>Loxodonta africana</i>		3	Mammal
Chacma baboon	<i>Papio ursinus</i>		2	Mammal
Anchieta's cobra	<i>Naja anchietae</i>	2		Reptile
Brown forest cobra	<i>Naja subfulva</i>	1		Reptile
Mozambique spitting cobra	<i>Naja mossambica</i>	1		Reptile
Snouted cobra	<i>Naja annulifera</i>	1		Reptile
Black spitting cobra	<i>Naja nigricincta</i>	1		Reptile
Nile crocodile	<i>Crocodylus niloticus</i>	4		Reptile

5.5 Discussion

From our analyses, it was clear that southern African pythons are managing to persist across large areas of South Africa, with more reports and localities in recent years than historically, despite ongoing anthropogenic land-use changes. This, however, is likely a symptom of citizen science and greater access to platforms for reporting sightings than of the species' actual increase or expansion. As would be expected from a large-bodied ectotherm, pythons favour areas with

medium-high rainfall and lower elevations with suitable vegetation cover and mild winters. They face a diverse array of threats at all stages of their life cycle, both anthropogenic and natural, and while they persist in South Africa, they are under serious pressure as a species.

5.5.1 Southern African python occurrence

The distribution of the southern African python records in South Africa over the two periods was not markedly different. However, there were significantly more records from the second time period (2015 to 2025) than the first (1907 to 2014); however, these extra localities “filled in the gaps” rather than identifying distinctly new areas. It is essential to note that the “before” data set spans records from 1907 to 2015, whereas the second data set covers only a 10-year period. In the early period, the areas with the most records were for the most part within government protected areas, including Kosi Bay Nature Reserve, Ndumo Game Reserve, Tembe Elephant Park, St. Lucia Wetland Park and Kruger National Park, which is explained by the Ezemvelo KZN Wildlife database and the accurate record keeping that was carried out by members of staff stationed in these reserves. Additionally, large numbers of guests visited these parks, while scientists conducted research within the parks/protected areas (Martin et al. 2025). Visitors to protected areas are more likely to report sightings than residents living outside protected areas. The more recent data set, with almost double the number of records, was partly a result of citizen science and researchers’ access to platforms like Facebook® and iNaturalist® for extracting information. These occurrence distribution maps for the two periods also demonstrated the value of such platforms for research, as previously noted, especially for cryptic or difficult-to-work-with species (Maritz and Maritz 2020; Kyle and Downs 2025). From the vegetation data, it was apparent that southern African pythons favour well-vegetated areas in South Africa, specifically forests and

savannas, characterised by lush vegetation. The diverse vegetation types in which they were observed also illustrated that the southern African python shows behavioural plasticity and is a versatile species. There is currently a discussion that South Africa's forests are technically more densely vegetated savannas, which aligns with pythons' habitat preferences (Adie et al. 2017, 2023).

The vegetation data were analysed using two methods, both of which had biases. The number of sighting records was influenced by observer bias; for example, game reserves would have a higher visitor rate than private farmland, where few sightings would occur. While the grid cell method was biased by the size of the grid cells, which were quarter-degree, in line with the red data listing. This meant that the fine-scale vegetation map was rendered inaccurate as the resolution was too coarse. The results showed that for finer-scale habitat work, grid cells were not always the most accurate method. Smaller grid squares would certainly yield more accurate analysis; however, this should be borne in mind when conducting such research.

Southern African pythons occurred over a wide range of elevations, from sea level to over 1,700 m.a.s.l. However, a higher proportion was found at lower elevations than at higher ones.

The two time series' localities of southern African python were almost equally distributed between protected and unprotected areas, suggesting that these snakes have a remarkable ability to persist in unprotected areas, despite numerous threats of anthropogenic origin, for example, roads, fences, harvesting, wanton killing and fires (Tolley et al. 2023; Cormac et al. 2025). Considering that only 9.2% of South Africa's mainland surface area is classified as protected (South African National Biodiversity Institute 2021), it becomes apparent that, although the numbers for protected and unprotected area localities are almost equal, the amount of the protected and unprotected land is not. The density of sightings within protected areas was higher than in

unprotected areas. This potentially indicates two points: firstly, if high numbers of pythons are still being found there, then these protected areas are working for the species, and secondly, they are being persecuted outside these protected areas and thus require greater legal protection.

5.5.2 Threats

Snakes as a group are under pressure and are declining globally at an alarming rate (Reading et al. 2010), including Africa (Farooq and Geldmann 2024), and particularly in South Africa (Schmidt 2018). Evidence suggests this might also be the case for southern African pythons (Green et al. 2022; Kyle and Downs 2025).

A literature search yielded little information on predation on southern African pythons. There was a one mention of warthogs (*Phacochoerus africanus*) killing them – assumed to be in defence of their young (Broadley 1983) and a short note detailing large predators, particularly leopards, eating them, and adding a further ten accounts of leopards killing pythons, one account of a lion (*Panthera leo*) and two more accounts of hyena (presumably spotted) (*Crocuta crocuta*) (Branch 2016). This short note also mentioned leopards killing them without eating them (Branch 2016). Alexander (2007) also recorded a large python being killed and not eaten by a banded mongoose.

While southern African pythons are well known as important predators (Broadley 1983; Marais and Kemp 2022; Kyle and Downs 2025), they also serve as a food source for many species, as illustrated by predation records from this study. They also appear to be recognised as a threat by certain other animals, specifically leopards, baboons, elephants and mongooses. In the mongooses' and baboons' case, it could be a case of killing the snake before it killed them, as pythons are recorded eating both banded mongooses and baboons (Kyle and Downs 2025). In the

case of leopards, several instances were documented in which leopards ate southern African pythons, indicating a predator-prey relationship (Branch 2016). However, other instances were recorded where the leopards killed the snakes, leaving their bodies uneaten. This behaviour is also observed in relation to other predators, such as the cheetah (*Acinonyx jubatus*) (Mills and Mills 2014), and has been described as resource guarding. The leopards may recognise the pythons as a threat to their food resources, particularly as both favour impala, as mentioned by Branch (2016). The elephants cannot be explained by either predation or resource guarding. All accounts originated from Tembe Elephant Park and spanned a thirty-year period. Southern African pythons pose no real threat to adult elephants, but elephants are recorded as showing aggression to other animals (including predators) (Allen et al. 2021), and this may simply be an extension of that behaviour or even a generalised snake response.

Cobra species apparently are a threat to small, juvenile pythons; the black spitting cobra (*Naja nigricincta*) was even observed raiding a python's nest hole and eating several of the neonates before they had left the burrow. The four instances of Nile crocodile (*Crocodylus niloticus*) predation are interesting as both reptiles favour water bodies and are generalist predators, suggesting that the predation of the crocodiles on the pythons serves the purpose of resource guarding as well as a meal.

Fires are a particular threat to southern African pythons because most fires happen in late winter. Snakes are especially vulnerable at this time of year, as they are generally slow-moving and, because of the lower temperatures, spend time basking in the sun (Alexander 2007). Literature states that this is the time when pythons appear to congregate for extended periods of time for breeding purposes (Alexander 2007), which could result in several snakes being killed in a single burning event, as occurred in Tembe Elephant Park (Jordaan and Steyl 2022).

Linear infrastructure, particularly electric fences and roads, poses a threat to southern African pythons (Tolley et al. 2023; Cormac et al. 2025). Despite the limited number of records available concerning fatalities on electric fences, the IUCN (Tolley et al. 2023) and a 2009 study (Beck 2009) recognise them as a threat to pythons. Their prey is swallowed whole and is frequently large, resulting in a greatly distended body. In normal conditions, without the feeding bulge, they are able to use familiar routes and slither under electric fences without being shocked; however, having ingested large prey items, they can get stuck under these fences. They are then unable to escape due to the wire pinning them down, and as a result, are electrocuted.

Roads are a major threat to southern African pythons (Schmidt 2018). Their long bodies and generally slow movement make them particularly vulnerable to vehicles (Cormac et al. 2025). This is exacerbated by their propensity to move at night, which renders them less visible. Due to an innate fear that many people have of snakes (Ohman and Mineka 2003), and even pythons in particular (Kyle and Downs 2025, 2026), combined with the financial value placed on these snakes, there is a strong likelihood that some drivers would actively aim to kill pythons, as well as accidental strikes that happen when drivers do not see them.

A threat to southern African pythons, which is extremely difficult to quantify but is known to be substantial, is the traditional medicine or ‘*muthi*’ trade (Tolley et al. 2023). Pythons hold an important place in many African cultures and beliefs and are still used in multiple “traditional medicine” practices (Kyle and Downs 2025, 2026). *Muthi* markets and practitioners are notoriously reluctant to impart information, being guarded and largely unwilling to participate (Williams and Whiting 2016). This renders the actual number of pythons killed for the *muthi* trade difficult to estimate. Tolley et al. (2023), in the most recent IUCN listing, recommended that this be quantified in some way. In contrast, Green et al. (2022) were able to establish that pythons are

among the top 10 species of animals used in *muthi*, as reported by the participants in their study. They also highlighted that pythons have become considerably harder for practitioners to access over the past five years (Green et al. 2022), a comment that warrants attention and concern.

Considering that southern African pythons have a wide distribution and occur extensively in inhabited areas, it is likely that these populations will have been depleted as is suggested by their scarcity in the “*muthi*” trade (Green et al. 2022). Now that these populations are reduced, it is likely that the pressures on protected areas will increase as the value of the snakes increases because of their scarcity.

5.5.3 Mitigating measures

Mitigating measures for southern African pythons include the management of burning of firebreaks or veld, which could include the timing of management fires to avoid the times of day when snakes are most likely to be out basking and thus most vulnerable to the fires, as well as the periods when snakes are likely to be massing for breeding events. In winter, snakes will be slowest and least responsive in cold weather and early in the morning when they are just emerging to bask. Fires set when snakes are warmer and more responsive would be preferable. Literature and unpublished evidence suggests that pythons congregate for breeding events from June to the beginning of October, depending on the area, thereby increasing the risk of multiple fatality events during these months. These snakes are also intent on breeding and, as a result, are less alert and responsive to potential threats, making them more vulnerable. Their breeding is however often associated with burrows, which would provide protection from the fires if they were situated in the burrows or able to retreat during the fire. Jordaan and Steyl (2022), however suggest that

significant damage is caused from smoke inhalation as well as the damage caused by the flames, meaning that the underground refugia might not be as effective.

Electric fences could be adjusted slightly, allowing southern African pythons to pass underneath, or the bottom wire could be set as a return/ground wire, which does not carry a current. Another option would be to reduce the time between pulses, allowing snakes to feel the first shock and retreat before they push too far under the wire, where they become stuck and are unable to escape between the multiple pulses that ultimately kill them. These methods could potentially also reduce fatalities in several other species that share a similar vulnerability to electric fences, for example, tortoises and pangolins, as has been mentioned in other studies (Lee et al. 2021)

Road signage and awareness could reduce road fatalities of southern African pythons, especially in areas with high python densities or those known to be roadkill hotspots. Knowing that pythons favour savanna and forested areas, most likely within protected areas, speeds could be reduced further in likely crossing areas. Awareness signage, notifying travellers that they might encounter either wildlife or specifically snakes, would be beneficial in these high-risk areas, increasing drivers' awareness and, hopefully, reducing the chances of unplanned collisions, as has been shown to be successful elsewhere (Van der Merwe 2019). We recommend that possible future research be done to monitor the effectiveness of these mitigating measures if they are applied.

5.5.4 Conclusions

It is clear that southern African pythons are persisting in South Africa despite anthropogenic land-use changes and other threats, and are still frequently observed in a large part of the country. However, it is also clear that they are facing a large number of threats, both anthropogenic and

natural. Their continued abundance within protected areas is a positive sign that, hopefully, a sufficient number of pythons will be able to persist to repopulate surrounding areas where they are being depleted for various reasons. Few people remain neutral towards such a large and iconic animal, either hating or fearing it because of its size and/or ability to eat pets and livestock, or loving it for the ecosystem services it provides and the important ecological role it plays (Kyle and Downs 2026). With this in mind, they are a good candidate as an ambassador or champion species that requires additional measures of protection, such as road signage and changes to electric fence design. Despite the fact that these snakes appear to be persisting in this rapidly changing environment, they need all the help and protection that they can be afforded if they are to continue to persist and even thrive.

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

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Appendix 5.1. Table comparing the results of the grid cell analysis method and the sightings record analysis method for southern African python vegetation type preference.

Vegetation type	Grid squares available	Grid squares occupied	Number of records
Andesite Mountain Bushveld	17	1	
Carletonville Dolomite Grassland	34	11	
Central Free State Grassland	3	21	
Central Sandy Bushveld			59
Crocodile Gorge Mountain Bushveld			4
Delagoa Lowveld			8
Dry Coast Hinterland Grassland	2	1	
Dwaalboom Thornveld	25	9	2
Dwarsberg-Swartruggens Mountain Bushveld	7	3	3
Eastern Valley Bushveld			33
Escarpment Arid Thicket	11	1	
Gabbro Grassy Bushveld			9
Ghaap Plateau Vaalbosveld	10	1	
Gold Reef Mountain Bushveld			8
Gordonia Duneveld			1
Grahamstown Grassland Thicket	7	1	
Granite Lowveld	22	15	142
Ironwood Dry Forest	4	3	
Ithala Quartzite Sourveld	3	2	
Kaalrug Mountain Bushveld			1
KaNgwane Montane Grassland	6	2	
Kathu Bushveld	8	2	
Kimberley Thornveld			1
Koranna-Langeberg Mountain Bushveld			1
Kuruman Mountain Bushveld	30	3	1
Kuruman Thornveld			1
KwaZulu-Natal Highland Thornveld	3	3	
KwaZulu-Natal Hinterland Thornveld			40
KwaZulu-Natal Sandstone Sourveld			10
Lebombo Summit Sourveld			3
Legogote Sour Bushveld			16
Leolo Summit Sourveld	1	1	

Limpopo Ridge Bushveld			6
Limpopo Sweet Bushveld	8	3	18
Loskop Mountain Bushveld			6
Loskop Thornveld			2
Low Escarpment Moist Grassland	3	2	
Lowveld Riverine Forest	6	3	
Lowveld Rugged Mopaneveld			7
Mafikeng Bushveld			2
Makatini Clay Thicket			17
Makhado Sweet Bushveld	9	4	8
Makuleke Sandy Bushveld	5	3	3
Malelane Mountain Bushveld			1
Maputaland Pallid Sandy Bushveld			13
Marikana Thornveld	1	1	11
Molopo Bushveld	22	3	4
Moot Plains Bushveld	1	1	7
Mopane Basalt Shrubland	2	1	9
Mopane Gabbro Shrubland			5
Morokweng Thornveld	1	1	
Musina Mopane Bushveld	10	4	12
Muzi Palm Veld and Wooded Grassland			4
Non-terrestrial (Aquatic)	2	2	
Non-terrestrial (estuarine habitat)	50	24	
Norite Koppies Bushveld			1
Northern Afrotemperate Forest	36	6	
Northern Coastal Forest	1	1	
Northern Drakensberg Highland Grassland	1	3	
Northern KwaZulu-Natal Moist Grassland	9	6	
Northern Lebombo Bushveld	14	11	8
Northern Zululand Sourveld			14
Ohrigstad Mountain Bushveld			3
Paulpietersburg Moist Grassland	5	3	
Phalaborwa-Timbavati Mopaneveld			10
Pilanesberg Mountain Bushveld			1
Polokwane Plateau Bushveld			13
Pretoriuskop Sour Bushveld	4	3	9

Rand Highveld Grassland	23	4	
Roodeberg Bushveld	13	3	5
Scarp Forest	45	22	
Sekhukhune Montane Grassland	2	1	
Sekhukhune Mountain Bushveld			2
Sekhukhune Plains Bushveld			1
Southern Lebombo Bushveld			9
Southern Mistbelt Forest	54	14	
Soutpansberg Mountain Bushveld	2	1	22
Springbokvlakte Thornveld			23
Stella Bushveld			4
Strydpoort Summit Sourveld	3	2	
Subtropical Alluvial Vegetation	47	27	
Subtropical Seashore Vegetation	3	1	
Swamp Forest	1	1	
Swaziland Sour Bushveld			14
Tembe Sandy Bushveld			8
Thukela Thornveld			4
Thukela Valley Bushveld			32
Tsende Mopaneveld			5
Tshokwane-Hlane Basalt Lowveld			59
Tzaneen Sour Bushveld			7
Vaalbos Rocky Shrubland	6	1	
Vredefort Dome Granite Grassland	4	2	
Vryburg Thornveld			4
Waterberg Mountain Bushveld	4	1	16
Waterberg-Magaliesberg Summit Sourveld	13	11	
Western Maputaland Clay Bushveld	1	1	29
Western Maputaland Sandy Bushveld			5
Western Sandy Bushveld			32
Woodbush Granite Grassland	1	1	
Zeerust Thornveld			10
Zululand Lowveld			62

CHAPTER 6

General discussion, recommendations, and conclusions

6.1 General discussion

Important factors affecting herpetofauna in recent decades include land use changes, toxin release into the environment, overexploitation, invasive alien species and synergistic interactions with climate change (Urbina-Cardona 2008). Of all the terrestrial vertebrate groups, reptiles are the most species-rich group, and yet little research has been conducted on them compared with other taxa (Urbina-Cardona 2008; Tingley et al. 2016), with considerably more work having been conducted on mammals and birds than on reptiles, amphibians, and fish (Bonnet et al. 2002).

Certain taxonomic groups are more challenging to study than others, and research on elusive species can be extremely demanding, requiring more time, effort, and resources than for less secretive species (Durso et al. 2011). Ectothermy, with its resulting reduction in movement and feeding frequency, renders such species particularly challenging to research, resulting in ectotherms being underrepresented in the literature (Miranda et al. 2013; Maritz et al. 2021). This is especially true of herpetofauna, because of their discrete and infrequent feeding habits and cryptic natural histories (Shine and Bonnet 2000; Steen 2010; Durso and Seigel 2015)

Even within these lesser-researched groups, bias has been recognised towards larger animals, species with wider distributions, non-fossorial species, and non-arboreal species (Guedes et al. 2023). According to these criteria, the southern African python (*Python natalensis*), the largest snake in southern Africa, occurs in multiple countries and is ground-dwelling; it should be one of the better researched species, however, this was found not to be the case (Kyle and Downs 2025a).

Southern African pythons are notable for several reasons, including their size, diet, often living in close proximity to humans, and their complex and varied interactions with humans. As the largest snake in southern Africa, they are also one of the top four largest snakes in the world (Murphy and Crutchfield 2019); historically reaching over 6 m, but in recent years mostly less than 5 m (Marais and Kemp 2022). They are one of the few snakes known to consider humans as prey, although few fatalities have been recorded (Branch and Haacke 1980), despite their continued persistence in close proximity to human habitations (Kyle and Downs 2025b). They are known to frequently prey on domestic species, either in livestock enclosures or while ranging in the veld, as well as pets, and are hated and persecuted for this (Kyle and Downs 2025c; Kyle and Downs 2025d). As generalist predators that occur in relatively high densities when conditions permit, they play a crucial ecological role in the populations of a surprisingly large number of species. They also have substantial cultural significance for many different people groups throughout their distribution, ranging from near deities in some, to curiosities, arch-enemies, revenue sources, or food sources in others (Kyle and Downs 2025d).

In a manner of speaking, the cards are stacked against *P. natalensis* as a species, with numerous factors contributing to its persecution, exploitation and decline. While the size or age of sexual maturity is not documented for southern African pythons, the literature suggests that females become sexually mature at a large size, exceeding 3.5 m (Branch and Erasmus 1984; Alexander 2018). Being large-bodied makes them more likely to be targeted by poachers (Benítez-López et al. 2019). A relatively slow growth rate (Alexander 2018) and large size before reaching sexual maturity mean that females must survive for a long time to replace themselves ecologically. Their extensive and involved breeding process also puts them at high risk, with numbers of mature snakes basking in the same areas for extended periods and leaving obvious signs of their presence

(e.g., spoor, basking sites, etc.). This makes them particularly vulnerable to fires, predation and poaching. The female's lengthy maternal investment, during which time she loses significant body condition, also results in weakness or mortality (Alexander 2018). The large sizes these snakes attain increase their risk of being killed on roads or on electric fences. Poaching has reduced the number of potential prey items in savanna biomes (Lindsay et al. 2013), forcing larger snakes to turn towards anthropogenic sources of food and so increasing the likelihood of persecution.

The traditional medicine (*muthi*) trade is recognised as being a significant and unpredictable threat to *P. natalensis* (Tolley et al. 2023). Python parts are known to be traded for a variety of uses, including both healing and harming consumers (Williams and Whiting 2016; Green et al. 2022; Kyle and Downs 2025d). According to one study, pythons are among the top four species most difficult to obtain (Green et al. 2022), thereby rendering them more valuable and sought after.

The overall aim of this study was to assess the persistence of the southern African python in South Africa, determining the threats faced and establishing baseline information about their life history, as well as documenting their anthropogenic significance (Chapter 1). The objectives were:

1. To establish and list the literature and information already published about southern African pythons and the genus *Pythonidae*.
2. To determine the southern African pythons' diet and the hunting methods employed.
3. To establish the overall perceptions and attitudes towards pythons in KwaZulu-Natal and South Africa, what specific negative and positive beliefs are held about them, how informed the public is about them, and whether people are aware of the ecosystem services these snakes provide.

4. To establish if they are persisting in South Africa in the face of marked land transformation and what specific anthropogenic and natural threats they face
5. To determine their vegetation type preference and whether they are occurring and persisting within protected areas or public areas. (Chapter 1).

6.2 Summary of findings

Chapter 2 was a systematic literature review of the reptile family Pythonidae, comprising 38 species across 11 genera. A total of 512 peer-reviewed publications related to the family, with the first dating back to 1844. The number of publications increased slowly until 2000, after which a rapid increase was observed. The majority of the research was conducted on single species, mostly on captive animals. The most researched species was *Python regius*, accounting for 37.7% of the papers. The most popular topic of research related to medical aspects, including anatomy, development, medication, nutrition, and digestion. Many species were found to be underrepresented in the literature, frequently corresponding to those listed as Data Deficient on the IUCN Red List. It was also highlighted that the majority of work (60.1%), which was conducted on snakes in captivity, had little relevance for the conservation or protection of these snakes in the natural environment. As such, future work should focus on underrepresented species; however, there is a dearth of information on wild specimens for even the most extensively researched species (*P. regius*).

According to the research findings, southern African pythons are underrepresented in literature, especially considering their size and ecological importance (Chapter 2). This finding aligns with other research highlighting a lack of research in the Global South (Downs et al. 2021), as well as in African herpetology (Tolley et al. 2016; Maritz et al. 2021), and specifically on

pythons (Kyle and Downs 2025a). A marked trend towards research on captive specimens was evident, which has important ramifications for the conservation and management of species, where decisions cannot be accurately and adequately informed by findings made on specimens in captivity. While some results can be expected to be replicable between captive and wild specimens (Neill 1960), others are not (Fisher et al. 2015), implying that for a comprehensive understanding of a species, its needs and its threats, research must be conducted on species in the wild.

Chapter 3 investigated the diet and feeding behaviours of the southern African python. Historical data, anecdotal information from credible individuals, and data collected from citizen science platforms (e.g., iNaturalist®) and social media platforms (e.g., Facebook®) were used to compile this list and gather the information. This resulted in a list of 104 vertebrate species that southern African pythons are known to feed on. An ontogenetic shift was found with a transition from avian prey species in smaller snakes to more mammalian prey as they grew and matured. These data revealed a more active hunting style than the ambush predators they were historically considered to be, as well as the use of hunting techniques such as caudal luring to attract prey to within striking range. Social media has been found to be a helpful tool for gathering data for projects of this nature; however, it is not a failsafe approach, and researchers need to have a solid grounding in the topic they are researching to effectively evaluate the data they gather and extract the maximum value from it.

Citizen science and social media were used to gather data for several aspects of this study, especially the southern African python's diet, persistence and threats (Chapters 3 and 5). With social media becoming more popular as a source of data (Lopez et al. 2019; Maritz and Maritz 2020), it was concluded that it is more useful for some species than others (e.g., larger, more well-known species), and that some platforms are more useful than others (e.g., Facebook® and

iNaturalist®) (Chapter 3). There are limitations to the information that can be extracted from these data sources, and it needs to be retrieved and analysed circumspectly; a prior understanding of the species is essential. However, within these limitations, and with mitigating measures applied, it can be a veritable mine of information, with more and more records being added with time.

While southern African pythons were known to be generalist predators, the extent of their plasticity was not previously understood, as they have both a highly varied diet and are flexible in their hunting and feeding modes (Chapter 3). This mixed foraging strategy is known from several species of snakes and is often linked to differences in environmental parameters (temperature, rainfall) or classes (age, sex, size) (Balent and Andreadis 1998). Southern African pythons were found to feed on species from all vertebrate classes, with the greatest diversity observed in medium- and large-sized individuals (Chapter 3). This could, however, be explained by the size of the snakes and that of the prey items, with smaller prey items being eaten more quickly and smaller snakes being harder to see and thus record. The ontogenetic shift from birds to more mammals, as snakes mature and grow larger, is relatively well-documented in snakes (Hampton 2018), including other members of the family Pythonidae (Murphy et al. 1978; Natusch and Lyons 2012). An increase in human-animal conflict was observed as the pythons grew larger, which could be attributed to the reduction in suitable naturally occurring prey items, forcing these larger snakes to prey on livestock (Chapter 3). This livestock raiding also demonstrated a hunting technique in which snakes actively move to, and return to, areas where they know prey items can be found, rather than simply waiting in ambush as was previously thought (Broadley 1983). Several novel hunting techniques were documented, including scavenging and caudal luring, as well as providing further evidence to existing information on pythons eating bird eggs and catching

fish from traps (Bruton and Cooper 1980; Alexander 2012). This behavioural plasticity demonstrates the adaptability of these predators (Chapter 3).

Chapter 4 detailed the results of a questionnaire conducted primarily in KwaZulu-Natal, inquiring about the attitudes and perceptions of the population towards southern African pythons. Respondents also provided information about any other interesting observations related to breeding and burrow use that they might have, as well as their feeding records. A total of 438 completed questionnaires were obtained from varied geographic and demographic backgrounds throughout South Africa. Surprisingly, the majority had a positive attitude and perception towards these large reptiles; however, it was apparent from many of the answers that there is still a great deal of fear and superstition surrounding this species. Some of the beliefs around pythons, as well as their “uses” in traditional medicine (*muthi*), were documented. Finally, a bilingual (in English and isiZulu) infographic poster was created to address some of the common misconceptions and myths surrounding this species.

Surprisingly, a mostly positive attitude towards southern African pythons was apparent amongst respondents to the questionnaires (Chapter 4). The word choice used to describe pythons was insightful, with many individuals recognising the important role they play as both pest control and a part of the food chain, serving as both predator and prey. They were also described as ‘beautiful’, ‘interesting’, and ‘important’, all words with positive connotations, while the negative words mainly evoked fear, danger, and even hatred (Chapter 4). The neutral words indicated a lack of knowledge and understanding, which was evident in the answers to some of the other questions asked. Many of the beliefs surrounding pythons are based on supernatural situations or actions that are physically impossible and untrue. This phenomenon has been documented in relation to snakes previously (Stanley 2008). The fear associated with snakes is deeply rooted and complicated, with

both innate and learned aspects (Ohman and Mineka 2003). All of this makes it extremely difficult to rationalise or change these beliefs; however, education can succeed, and these fears can be overcome (Gibbons and Dorcas 2005; Stanley 2008). The factors found to have a significant positive effect on the respondents' attitude towards snakes were increasing age, province of origin, employment, and having previously encountered pythons (Chapter 4). Exposure to snakes could potentially be addressed through educational campaigns (Chapter 4).

It was encouraging to see that most people are aware of some of the ecosystem services that pythons provide, although several of the answers indicated that their positive attitude towards pythons was caused by the revenue they could generate through illegal trade (Chapter 4). The uncertainty that arises from the use of cultural and traditional medicine (*muthi*) is interesting. This could be because of people not wanting to reveal their beliefs, or it could simply be a sign of younger people moving away from historic beliefs and cultural practices (Gupta 2024).

Questionnaires have many benefits, for example, they can reveal respondents' attitudes and feelings on a finer scale than other methods, and they can highlight and draw attention to areas and threats that researchers would not have been aware of. They do, however, have limitations that need to be considered when working with the resulting data. Biases are unavoidable, whether they are completed online or in person; either certain groups will be missed out because of a lack of access to online sources, or respondents will be influenced either positively or negatively by in-person interviews - so a baseline understanding of this reality is an essential starting point for a questionnaire project (Saris and Gallhofer 2013). Bearing this in mind, there are still benefits and insights that can best be gained by gathering data in this way. Perceptions and attitudes of people towards large animals are always a challenging topic, as people seldom remain neutral. It is essential to remember that the results of a project based on perceptions are simply what the

respondent thinks or feels about the species, rather than necessarily reflecting reality. Management recommendations stemming from such a study should thus take this into account.

Chapter 5 examined a dataset of southern African python locality records, which spanned two time periods: before and after 2015. This revealed that pythons have been able to persist over a similar range as historically, despite the agriculturalization and urban transformation that South Africa has and is experiencing. Multiple anthropogenic and natural threats faced by these species were documented, including predation, fire, electric fences, persecution, and roads, suggesting some mitigation methods that could be employed to better protect them and other species. Considering the vegetation type of the locality records, it was concluded that pythons appear to favour forest biomes, predominantly in low lying areas. The data chapter, pertaining to the persistence of southern African pythons in South Africa, provides valuable insights into the species and how it can be protected going forward (Chapter 5). Confirming that the species persists despite numerous serious threats is encouraging. There has been an increase in the amount of data available in recent years, largely because of the advent of social media, which provides an easy way for citizen science to contribute to records. From this recent data, it appears that they persist in a surprisingly large section of the country. The percentage of records from within protected areas was both encouraging as well as concerning, as clearly the protected areas are advantageous for them. It does imply, however, that either they have been heavily persecuted outside of these protected areas, or the habitat has been transformed and is no longer suitable for them (Chapter 5). Insights into their habitat preferences and requirements are valuable for further protection of this species, as they identify which environmental parameters create suitable habitat for pythons. The wide range of vegetation types demonstrated the diverse habitats in which the southern African python can survive, however it was clear from the data which the preferred vegetation types were.

Future protection of areas including these vegetation types would thus be most suitable for protecting these snakes.

The identified threats reveal the vulnerability of southern African pythons to anthropogenic activities (Chapter 5). While there are substantial direct threats, in the form of harvesting and simply killing, which need to be quantified and controlled, the indirect threats are potentially more dire, as they are less easily managed. There are several unprecedented threats that pythons face because of their persistence in transformed landscapes. The reduction and removal of naturally occurring ungulates, and thus natural food sources, from much of the landscape forces pythons to feed on domestic animals, increasing their risk of being discovered and killed by the people in defence of their livelihoods. Roads, fences, and fires, even with mitigating measures and the wisest application, will still have a significant negative impact on python populations because of aspects of pythons' nature and behaviour. Their consumption of large prey items and the resulting distended body render them slow and extremely vulnerable to threats while they are digesting a large meal. During this time, they also seek shelter, usually in holes or thick bush, and in the transformed landscapes, this shelter is often in sugarcane (*Saccharum officinarum*) fields, making them extremely vulnerable to sugarcane harvesting fires. Agriculture provides the coal face, so to speak, for human-python interactions, as this is where pythons and humans will most often encounter each other, both passively and actively. Pythons are attracted to livestock, as well as the favourable habitats that farmlands provide, with abundant cover, food, and water. Many farmers have a positive response to pythons, aware of the pest control services they provide; however, even on these 'python-friendly' farms, indirect killing often occurs through day-to-day farming procedures, such as the use of agricultural machinery in fields, the poisoning of crops, and the burning of fields.

Southern African pythons also face numerous natural threats and predators at all stages of their lives. The data revealed an important part of the food chain, in which young pythons serve as prey to several different species of birds, mammals, and, interestingly, reptiles, specifically snakes. The number of natural threats illustrates that pythons are adapted to persist despite a high off-take, possibly as a result of their large clutch sizes and maternal investment, which allows the neonates an enhanced possibility of survival.

Unfortunately, biases are present in the datasets. The locality and feeding data of southern African pythons are biased towards areas in which people are more likely to report sightings, such as nature reserves or areas where snake removers work. The questionnaire data is biased towards people that the authors could contact, such as those on mailing lists or Facebook® pages. Biases occur in most datasets, and yet they can still reveal useful insights and critical information, contributing to what is known. Valuable data can be retrieved from most situations, provided that biases are acknowledged and accounted for.

6.3 Recommendations

It is recommended that further research be conducted on these large, charismatic snakes, the southern African python (Table 6.1). There remain substantial holes in our knowledge of the life history of southern African pythons, which, if filled, would afford an improved understanding of and protection for the species. Little is known about their movement, home range, burrow use, and the age/size of sexual maturity, among other topics. Further work focusing on these aspects would be valuable and is suggested. Tolley et al. (2023) recommend that the use of pythons in the ‘*muthi*’ trade be quantified to some degree as well as controlled.

Education campaigns in schools and other rural areas should be carried out around these and other reptiles. It appears that ‘*muthi*’ uses for large reptiles are similar - for example, the fat of Nile monitor lizards (*Varanus niloticus*), Nile crocodiles (*Crocodylus niloticus*), and southern African pythons are all used for the healing of various skin and joint ailments (Phaka et al. 2023; Tolley et al. 2023). Therefore, it is recommended to explore the possibility of substituting oils and possibly other parts from wild specimens with those that could be sustainably sourced from commercial crocodile farms, thereby alleviating pressure on wild populations.

Spreading awareness about the ecosystem services that southern African pythons provide would be beneficial to their persistence; however, it is recommended that their value in the tourism trade be promoted. The interest and emphasis around reptile-based tourism is increasing globally, and with it, the potential for financial gain (Gohori 2024). Southern African pythons meet many tourism requirements, being potentially the largest snake on the continent, capable of consuming large prey items and even considered to be ‘man-eaters’. If snakes could be viewed as a source of sustainable revenue rather than their value as a single sale to the illegal trade, it would be beneficial for both snakes and the communities they inhabit.

Table 6.1: Illustration of the aims, key findings, and recommendations emerging from this study on southern African pythons.

Aims	Findings	Recommendations
Establish what research has been conducted on <i>Pythonidae</i>.	The vast majority of research is conducted on animals in captivity, with relatively little focus on species in the wild. Heavy research bias towards species of commercial interest. Many species have not been researched at all or with very few studies.	Conduct research on pythons in the wild, especially on Endangered and Data-deficient species. Focus on those with limited ranges and extensive threats to establish how to conserve them, as well as to determine their environmental requirements.
Establish what research has been conducted on <i>P. natalensis</i>.	Very little has been done on <i>P. natalensis</i> , with the existing research mainly focusing on thermoregulation and maternal care of young.	Focus research on other aspects of their life history, especially those with conservation and management implications, such as home range size.
Document the diet of <i>P. natalensis</i>	Using literature, observations, and citizen science, 104 different species of mammals, birds, reptiles, and fish were recorded as being eaten by pythons.	N/A
Identify hunting and feeding techniques	Pythons were documented using caudal luring, scavenging, and active hunting, and an ontogenetic shift was observed as they mature.	N/A
Assess the attitudes of South Africans towards pythons.	There was a surprisingly positive response towards pythons; however, those that were negative were vehemently so.	Emphasise the sustainable uses of pythons, for example, the ecosystem services they provide, as well as ecotourism potential
Document some of the cultural beliefs and uses of pythons.	Cultural beliefs are both positive and negative, and medicinal uses of pythons can be used to both heal and harm people. There is a strong association with power and ancestors.	It is suggest replacing pythons in the <i>muthi</i> trade with sustainable options, e.g., commercially farmed Nile crocodiles.
Gauge public knowledge of pythons and their impacts, positive and negative	Most are aware of the positive impacts of pest control, and several associated pythons with financial gain through trade. Most were aware of their raiding livestock	N/A
Assess persistence amid land transformation	Pythons were found to be persisting through much of their historic range; however, proportionally more were	Ensure that pythons are catered for in the existing protected areas.

	found within the protected areas than outside of them.	
Identify anthropogenic and natural threats	Established that 15 species of birds, mammals, and reptiles prey on and kill pythons, as well as direct and indirect anthropogenic threats, including fires, electric fences, roads, persecution, and harvesting, which are increasing.	Raise awareness about the impact that roads, fences, fires, and agriculture have on pythons, and where possible, enforce mitigating measures, such as raising bottom strands on fences, installing signage on roads, and timing burns.
Define environmental requirements.	The forest biome was found to be the most favoured by pythons, followed by the Indian Ocean Coastal belt. The highest proportion of records were also found in low elevations, although they were recorded from sea level all the way to 1800m.a.s.l.	Ensure that protected areas where pythons are thriving are managed specifically for pythons, ensuring that the habitat is not altered to become unsuitable for them, for example, by overstocking with large mammals.
Recommendations: Further research should be conducted on southern African pythons to fill important gaps in their life history, specifically around burrow usage and home ranges. To provide information to farmers and other invested and interested parties on how to protect their pythons. To address the <i>muthi</i> trade and attempt to establish sustainable harvesting and usage. To encourage the promotion of pythons in ecotourism, providing a sustainable source of revenue from the presence of large snakes.		

6.4 Conclusions

In conclusion, based on the information gathered and analysed throughout this study, the overall trend that has emerged is that southern African pythons are adaptable, intelligent animals that continue to persist in relatively high numbers throughout much of their range. That said, however, they are under extreme direct and indirect anthropogenic pressures, in addition to a plethora of natural predators and environmental threats. Because of this, as a species, they have adapted to survive considerable persecution; however, with the increase in linear infrastructure and land transformation forcing them into increasingly more contact with humans, it is unclear if they can persist in these changing landscapes into the future. Pythons are a specially protected species; however, this appears to have little impact on illegal trade and none on indirect anthropogenic threats, such as road mortalities and fires. Perhaps the best solution for these snakes is to protect more favourable habitats, enforce wise burning strategies and road use, and thus allow them to

reproduce and persist naturally in protected areas. In doing so, they may hopefully disperse into other non-protected areas of their range.

6.5 References

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