

**The diet and feeding ecology of the brown house snake, *Boaedon capensis***

**Ielhaam Bassier**

University of the Western Cape, Department of Biodiversity and Conservation Biology,  
Private, bag X 17, Bellville, 7535, South Africa.

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**Supervisor: Dr. Bryan Maritz**

**Co-supervisor: Dr. Robin Maritz**

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## Abstract

African brown house snakes (*Boaedon capensis*) are widely thought to be dietary specialists that predominantly consume rodents. Given their ubiquitous distribution, these snakes potentially play an important role in controlling rodent populations throughout their range. However, the full extent of the diet of this species remains poorly quantified, and the proportional importance of mammals to their diet is speculative. Moreover, little is known regarding intraspecific dietary variation of these snakes. In recent years, a dearth of reports of *B. capensis* feeding, particularly from novel information-sharing streams available through social media, suggests that the diet of these snakes may be broader than previously thought. *B. capensis* are not rodent specialists as amphibians (3%), birds (12%), and reptiles (38%) collectively comprise a significant proportion of their diet. There was no evidence for sexual size dimorphism or dietary variation between adult males and females. However, significant differences in morphology and prey utilisation between adults and juveniles indicate an ontogenetic shift in diet from small lizards to larger, and more diverse prey. Variation in climate and time of year did not affect diet. Importantly, the diet of *B. capensis* as presented by museum data vastly differed compared to literature and community science reports. In particular, the proportional use of reptiles differed across sources (museum data = 6%; community science data = 27%). Overall, my findings reiterate the importance of examining multiple sources of information when characterizing the diet of species, as these multiple sources provide different result outcomes.

## Keywords

*Boaedon capensis*; community science; data bias; dietary niche breadth; dietary variation; ecological function; foraging ecology; ontogeny; snakes; specialist vs. generalist predators



## Declaration

I declare that “**The diet and feeding ecology of the brown house snake, *Boaedon capensis***” is my own work, that it has not been submitted for any degree or examination at any university, and that all sources I have used or quoted have been indicated and acknowledged by complete references.

**Full name:** Ielhaam Bassier

**Date:** 9 November 2021

**Student Number:** 3238823

**Signature:** 



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The logo of the University of the Western Cape, featuring a stylized building with columns and the text "UNIVERSITY of the WESTERN CAPE".

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## **Chapter 1: Introduction**

### **1.1 Snakes as predators**

Snakes comprise a highly diverse lineage of approximately 3900 species distributed across the globe (Uetz et al. 2020). Each of these species are predators that eat other animals (Greene 1997). Collectively, snakes possess a range of unique morphological and ecophysiological adaptations that allow them to locate, capture, and consume a large selection of different types of prey varying in size by orders of magnitude from miniscule invertebrates to large mammals (Greene 1997; Cundall & Greene 2000). Most snakes are unable to reduce the sizes of their prey by biting off pieces and so are considered gape-limited. However, the unique adaptations that snakes possess, including highly kinetic jaw apparatus, allow these animals to display impressive feats of ingestion of large prey (Greene 1997; Gans 1983; Moon et al. 2019), which allows them to consume a variety of different organisms.

The diets of individual species of snakes can vary dramatically across different lineages. Diet is known to affect several aspects of snake ecology such as habitat use (Plummer 1981), distribution (Slip & Shine 1998; Colston et al. 2010), and activity patterns (Wasko & Sasa 2012). Moreover, diet is a major driver behind the diversification of snakes, and the radiation of novel lineages have been repeatedly facilitated through adaptive evolution relating to responses to different prey (Greene 1997), including adaptations of feeding apparatus (Gans 1952; Gans 1974) and venom composition (Daltry et al. 1996; Barlow et al. 2009; Lyons et al. 2020). Understanding snake diets can thus provide important context for understanding snake diversity and the roles of different snakes within ecosystems.

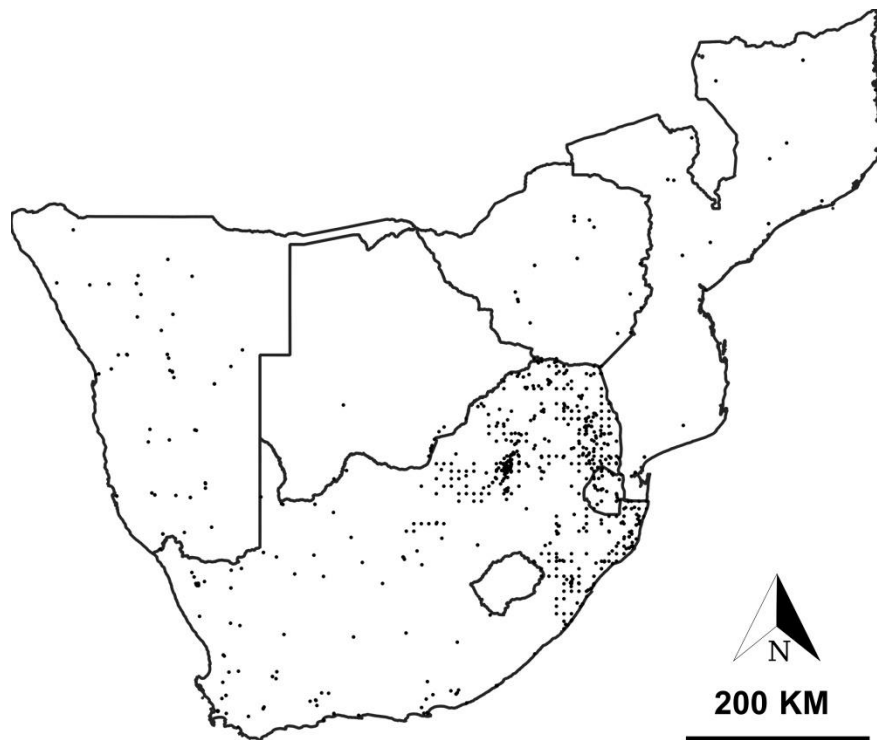
Many species of snake consume a variety of rodent species, including several species considered by humans to be pests (Branch 1998; Cundall & Greene 2000). In anthropogenic

areas, these snakes may therefore provide important pest control regulatory services that are beneficial to humans. Several rodent species are known carriers of diseases, pathogens, and various parasites, of which several pose a credible health risk to humans (Wodzicki 1973; Keogh 1985). Additionally, rodents also tend to consume large quantities of food and cause damage to human property, and in rural areas threaten crops and produce (Buckle & Smith 2015). By preying on such pest species in high densities, snakes potentially provide a beneficial pest control service to humans in the form of direct regulation of small mammal populations. The intensity at which such a service is provided undoubtedly varies between snake species. Unfortunately, the extent to which snakes affect their environments and ecosystem functions remain unclear for most species.

### **1.2 The brown house snake (*Boaedon capensis*)**

The brown house snake (Serpentes: Lamprophiidae: *Boaedon capensis*) occurs across most of southern Africa (Bates et al. 2014; Figure 1.1) occupying a variety of habitats and biomes (Marais 2004). Its range extends from South Africa through much of East Africa across Malawi, Tanzania, and Kenya (Hughes 1997; Spawls et al. 2018). However, the systematics of the *Boaedon capensis-fuliginosus* complex remains unresolved and the species boundaries of these snakes are poorly defined (Hallerman et al. 2020), meaning that the distribution of the brown house snake as we currently understand it may be incorrect. These snakes are found frequently in urban areas where they are often observed within people's homes (Branch 1998; Bates et al. 2014)—hence the common name of house snake. Brown house snakes are medium-sized (average adult snout-vent length: 900 mm; Marais 2004) constrictors that are thought to feed primarily on rodents (Branch 1998; Alexander & Marais 2007; Byars et al. 2010), for which they forage at night. Because brown house snakes are frequently observed in human-dominated landscapes (Alexander & Marais 2007), they may

potentially provide an important ecosystem service by regulating the population sizes of rodents frequently considered to be pests.



**Figure 1.1: Distribution of *Boaedon capensis* within southern Africa. Black dots indicate occurrence points obtained from [www.gbif.org](http://www.gbif.org).**

### **1.3 The unresolved feeding ecology of the brown house snake**

The diet of the brown house snake has been characterized as predominantly comprising of rodents (Broadley 1983; Marais 2004; Alexander & Marais 2007). However, several reports of brown house snakes preying on other taxa have cast doubts on our understanding of the full extent of the prey utilised by these snakes. For example, Broadley (1983) mentions that juvenile individuals will sometimes consume reptiles whereas the adults mostly consume rodents. Additionally, Branch (1998) states that in addition to consuming rodents, brown house snakes in arid regions often also consume lizard prey. The full spectrum of prey

utilised by brown house snakes remains unclear, and to date, no detailed examinations of their diets have yet been conducted.

Literature sources of dietary information for brown house snakes are also limited. The diets of these snakes have yet to be formally quantified and few sources of dietary data have been published. Additionally, field guides rarely reference specific prey, and instead, only provide broad classifications with no mention of specific species or proportions of different prey consumed (Broadley 1983; Branch 1998; Alexander & Marias 2007). However, some information on brown house snake feeding records collected from stomach dissection has been published (see Broadley 1966; De Waal 1977; Jacobsen 1989). One promising source of dietary information for these (and other species) is that of community science (Maritz & Maritz 2020). Because brown house snakes are commonly observed within urban environments, community science lends itself well to shareable observations of predation via widely used social media platforms.

#### **1.4 The challenge of mammal identification**

Studies attempting to quantify snake diets typically involve dissecting dead or preserved specimens to examine and identify prey remains found within their stomachs and intestines (Glaudias et al. 2017). In cases where prey remains are relatively undigested and remain whole or are largely intact, it is possible to use morphological characters (e.g., dentition, scales or claws) to identify species. However, this becomes difficult when prey remains only consisting of undigested clumps of hair. Quantifying the diet of a primarily mammal-eating snake like the brown house snake is therefore likely to be challenging and may in part explain why detailed accounts (with prey identified to the species level) of the mammals consumed by these snakes are scarce.



Identifying mammals from hair remains has been a challenge to biologists for several decades (Williamson 1951; Dryer 1966; De Marinis & Asprea 2006; Sessions et al. 2009).

Fortunately, a variety of techniques and methods have been developed in recent years which continue to improve our ability to identify species from hair remains. Most notably, identifications based on hair cuticle scale patterns have proved successful in prior works (e.g., Moyo et al. 2006; Glaudas et al. 2017). This technique incorporates assorted microscopy techniques (Verhoven 1972; Short 1978; Dagnall et al. 1995; Chattha 2011) and machine learning software (Meyer et al. 1997; Verma et al. 2002) to match the cuticular patterns of hair found in stomachs to known animals from existing catalogues and databases (Perrin & Campbell 1980; Keogh 1985; Cavia et al. 2008; Seiler 2010; Taru & Blackwell 2014).

### **1.5 Problem statement**

Brown house snakes, *B. capensis*, are abundant, widespread predators that potentially facilitate regulatory pest control services in the form of predation on rodents considered as pests. However, the full extent of the diet of *B. capensis* is poorly quantified, leaving several key questions about their utilisation of different prey unanswered. As such, the proportion and importance of rodents within the feeding ecology of these snakes remains speculative, and therefore any inferences of potential ecosystem services being performed by these snakes cannot be made with certainty. Moreover, the degree to which diet varies temporally or spatially is also poorly quantified despite hypotheses about these sources of variation in the literature.

### **1.6 Aims and objectives**

In this study, I attempt to quantify the diet of *Boaedon capensis* using a combination of literature sources, dissection and microscopy techniques, and social media community science predation records to provide a fine-scale assessment of the dietary composition of



these snakes. I develop a mammal hair cuticle scale pattern database against which to compare hair samples extracted from the stomachs of dissected animals, and critically evaluate the performance of a machine-learning tool for identifying hair samples. I further aim to compare how diet varies between sexes, ontogenetically, geographically, and temporally. Lastly, I aim to compare how the diets of these snakes are represented across different sources of information to assess biases in data collection processes.



## Chapter 2: Methods

### 2.1 Examination of museum specimens

I measured and dissected a total of 343 preserved brown house snake specimens from the collections housed at three South African Museums (Table 2.1). I measured the following morphological characters of each specimen: snout-vent length (SVL), tail length (TL), head length (HL), head width (HW), and head height (HH). I measured SVL as the straight-line length of the snake from the tip of its snout to the cloaca using a tape measure, with the remainder of the snake being recorded as the tail length. I measured all head dimensions using digital calipers. I classified head length as the distance from the snout to the posterior margin of the lower jaw. I classified head width as the distance between the widest parts of the head measured dorsally. I classified head height as the distance between the bottom of the jaw to the top of the head. All measurements were to the nearest 1.0 mm. I recorded the mass of each specimen using a digital scale, taken to the nearest 1.0 g. In some instances, specimens were damaged to such an extent that measurements could not be made for some morphological traits and so the final sample sizes of recorded measurements are not evenly spread across traits. I also classified each specimen as either an adult male, adult female, or juvenile (<500 mm SVL) based on the presence of hemipenes or hemipene canals in males. For each specimen, I made a mid-ventral incision and removed all prey remains from within the stomachs and intestines of snakes. In total, I collected 102 samples of prey remains from 101 individual snakes. I identified all prey remains to the finest possible taxonomic levels using a combination of morphological characteristics, including hair cuticle scale patterns (see below), teeth, and skull morphology for mammal remains, and scale morphology for reptiles. Additionally, for prey items that were only partially digested and relatively intact, I used characteristics such as size, colour, hair patterns and other morphological features to identify those prey.

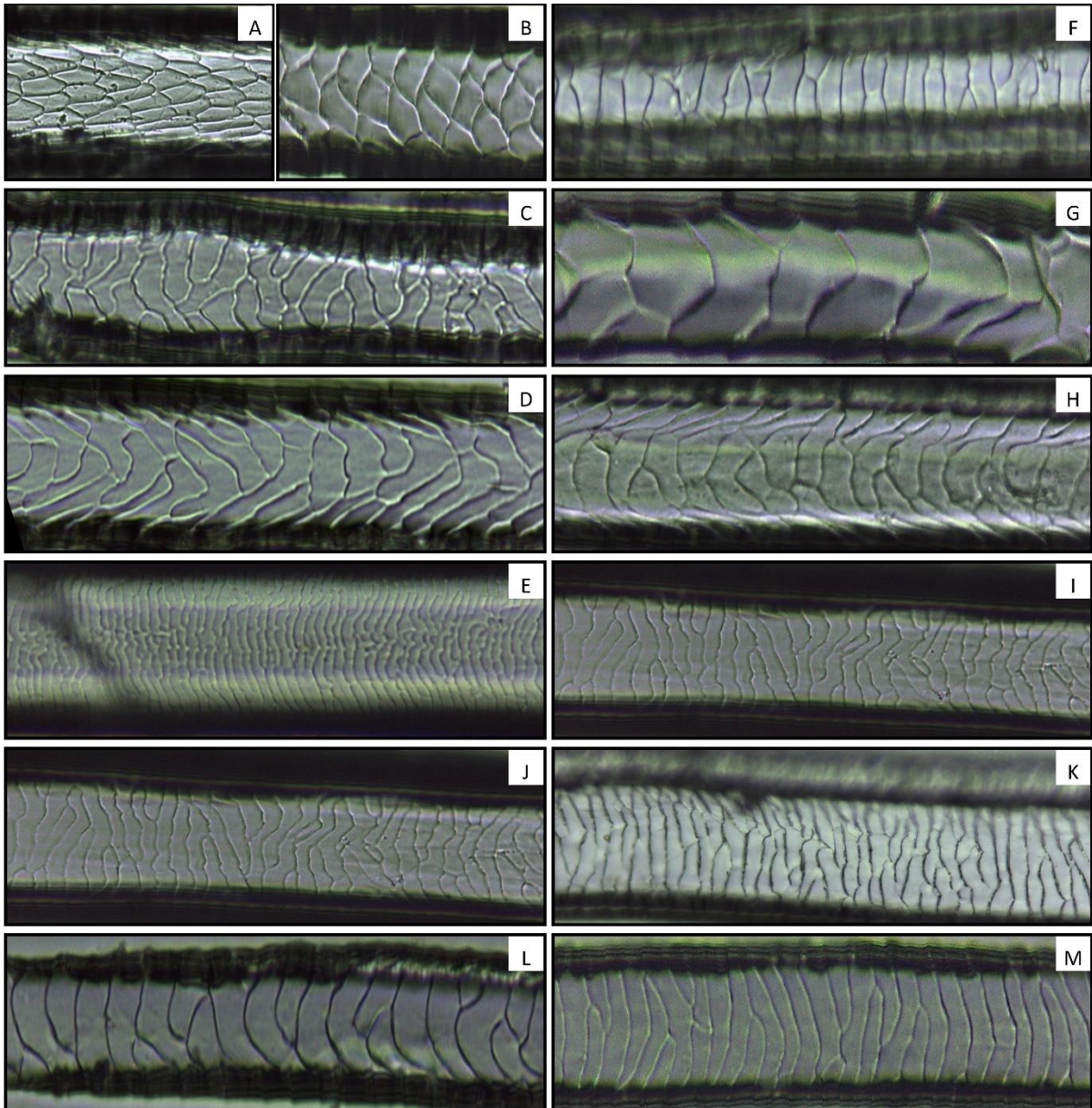
Table 2.1: Number of brown house snakes examined, and percentages of prey found per museum collection.

<b>Museum collection</b>	<b>No. snakes examined</b>	<b>% snakes containing prey items</b>
Bayworld	201	20
Ditsong National Museum of Natural History	46	43
McGregor Museum	96	43

## **2.2 Identification of hair samples**

### 2.2.1 Slide preparation of known and unknown samples

In several instances, the only remains of prey within the digestive tracts of specimens were small clumps of hair. To identify these, I relied on techniques derived from Foster et al. (2011) involving the hair cuticle scale patterns as the morphological characteristic for means of comparison. To obtain these patterns, for each sample, I cleaned all hair remains with distilled water to remove any inorganic and organic material and left them to air dry for 3–5 minutes. Thereafter, I placed a streak of clear nail polish (Revlon Colourstay) on a microscope slide and immediately placed a single strand of hair within the centre of the nail polish streak. The hair strand was left for 2–5 minutes to dry depending on the thickness of the nail polish application. Once the nail polish was completely dry, I carefully removed the hair with forceps, leaving behind an impression within the nail polish remaining on the slide (see Figure 2.1 for examples of hair impressions). This process was replicated 20 times per slide for each prey sample. I repeated the process 20 times to obtain different images from all sections of the hair for accurate analyzing in case of damaged hair. I used a confocal microscope to take high-resolution photographs of each sample at 40X magnification.



**Figure 2.1: Examples of hair impression reference slides to identify unknown samples.**

**A) *Rattus rattus*, B) *Mus musculus*, C) *Aethomys* sp., D) *Myosorex* sp., E) *Otomys irroratus*, F) *Crocidura* sp., G) *Mastomys natalensis*, H) *Micaelamys namaquensis*, I) *Rhabdomys* sp., J) *Saccostomus campestris*, K) *Eidolon helvum*, L) *Gerbiliurus paeba*, M) *Mus minutoides*.**

### 2.2.2 HairSnap validation

To identify mammal prey consumed by brown house snakes using only hair remains found in dissected specimens, I created and compared images of hair cuticle scale patterns of known



and unknown mammals to a database of known species. To do this I used the HairSnap plugin (Moyo et al. 2006; Foster et al. 2011) within ImageJ software (Foster et al. 2011). HairSnap employs a machine learning algorithm that analyses images of hair cuticular patterns to match them against known samples from a trained dataset of reference images of known species. I built a training dataset of mammals using 1087 images across 25 species of rodents and bats that occur throughout southern Africa. These images comprised photographs of prepared slides of hair cuticle scale patterns taken at different sections of hair strands (e.g. the root of the hair, the tip of the hair etc.). Additionally, this database was supplemented with 21 additional images of hair cuticle scale patterns obtained from the Urban Caracal Project (<http://www.urbancaracal.org>).

To test and validate the efficacy of HairSnap, I compared known samples of rodents to the training dataset. I calculated the percentage of replicates from each sample allocated to the same species. I expected that if the analysis worked appropriately with the samples provided, then all known-origin hair samples would be correctly identified, and within a single sample of stomach content hair, all (or most) replicates would be identified as belonging to a single species. Following these validity tests, I compared unidentified hair samples to the training dataset to identify those species to the lowest possible taxonomic level.

### **2.3 Social media sources**

I gathered several dietary records of brown house snakes feeding from community science reports through social media sources. I collated community science reports of predation records (Maritz & Maritz 2020) of brown house snakes posted online within the Facebook group “Predation Records – Reptiles and Frogs (sub-Saharan Africa)”. These reports took the form of online photographs of brown house snakes feeding or attempting to feed on a variety of prey under natural conditions (i.e., not in captivity). Because new records are frequently

added to this group, for the purposes of this study I had to decide on a stopping point at which to collate data. My final tallying of feeding records from this group thus concluded on 31 October 2019.

## **2.4 Literature survey**

I collated dietary records brown house snakes from the literature, including peer-reviewed publications, unpublished academic theses, and assorted society newsletters. Searches were performed using Google Scholar. I did not include information from field guides and secondary sources where descriptions of feeding were vague (e.g. “consumes rodents”). In all instances, prey taxonomies were updated to reflect their current nomenclature. I did not include records of captive feeding.

## **2.5 Dietary specialization**

I assigned each dietary record to a broadly defined taxonomic group of prey: amphibian, bird, mammal, or non-avian reptile (hereafter: reptile). To characterize the overall diet of brown house snakes, I used a one-way Chi-square test to compare prey type frequencies across prey groups to test the hypothesis that there is no difference in prey usage of the different prey groups by brown house snakes to infer if they are generalists or specialists. Additionally, I estimated Levins' measure of niche breadth (Levins 1968) using tetrapod level frequencies based on the formula:  $B = 1/\sum pi^2$ . For this equation,  $B$  = Levins' niche breadth and  $pi$  = the proportion of each prey type ( $i$ ). I then also standardized this to calculate a value ranging from 0 to 1 using the formula  $B_A = (B - 1) / (n - 1)$ . In this equation,  $B_A$  is the standardised niche breadth and  $n$  is the number of prey categories (Levins 1968).

I also tested the hypothesis that sampling method (museum, literature, community science) influenced the types of prey being reported in the overall diet. I did this by comparing the

proportion of mammal prey in the diet across the three sampling methods with chi-square analyses. I also calculated Levins'  $B_A$  values for each data source independently.

## **2.6 Morphological correlates of diet**

I quantified sex ratios and size class ratios respectively across specimens using two separate one-factor chi-square tests to compare frequencies of the various categories (adults vs. juveniles; adult males vs. adult females vs. unknown juveniles). To test for evidence of sexual size dimorphism in morphological traits between adult male and adult female brown house snakes, I performed a one-way ANOVA test to compare the average differences in SVL of male and female brown house snakes. I also performed five separate one-way ANCOVA tests using SVL as a covariate to account for differences in length between individuals to compare average differences in TL, HL, HW, HH, and mass respectively for those same groups.

To estimate the potential for an ontogenetic shift in prey consumption that could be present as a result of a shift in morphological sizes within brown house snakes, I compared the head morphology of adults and juveniles relative to their respective body sizes. For this analysis, I compared average head lengths of adults and juveniles using a one-way ANCOVA test with SVL as a covariate factor to account for body size. The head length was chosen as morphological evidence suggests that head length rather than head width is the main limiting factor of gape sizes in snakes (Cundall & Greene 2000).

To test the hypothesis that diet varies ontogenetically in *Boaedon capensis*, I used a one-way ANOVA test comparing the average SVL of all snakes containing prey items with prey type allocated as the grouping variable. Next, I tested the hypothesis that diet varies intersexually between brown house snakes by comparing proportions of prey categories utilised by adult males and adult females using a two-way Chi-square test.



## 2.7 Ecological correlates of diet

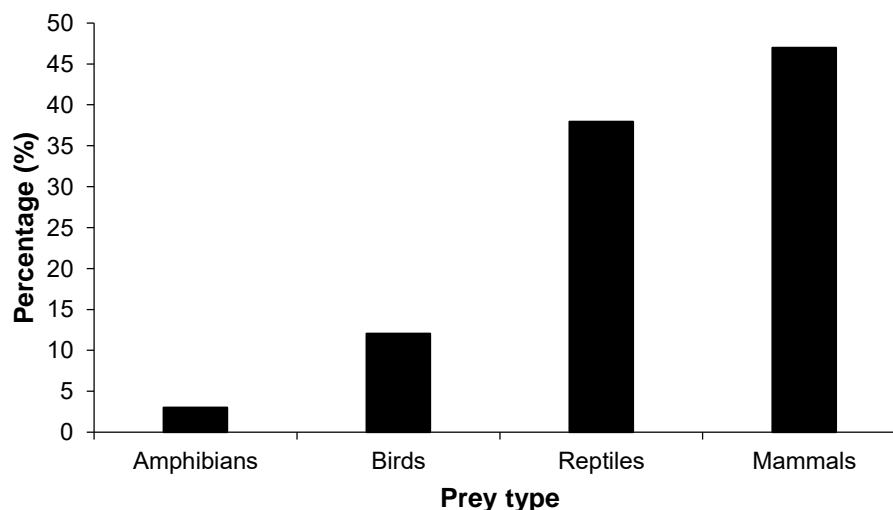
I tested the hypothesis that feeding occurs year-round within *B. capensis* by binning all predation records into the months of the year in which they occurred and comparing the proportions of these using a two way Chi-square test. Secondly, I made several comparisons between prey types and the climate and habitat in which they occurred. To obtain climatic information on temperature and precipitation I used bioclimatic layers obtained from Worldclim ([www.worldclim.org](http://www.worldclim.org)) (Bio 1 and Bio 12), and to obtain natural and rural classifications I used an urbanisation GIS layer obtained from the global rural-urban mapping project (<https://sedac.ciesin.columbia.edu/data/collection/grump-v1>). I plotted each of these layers within QGIS version 3.3 (QGIS Development Team 2018) and overlaid the GPS coordinates of all predation events for which location data were available. I then extracted the relevant temperature, precipitation, and habitat classification values at each GPS point using the point sampling tool.

I performed all statistical analyses using either SPSS software version 23 (IBM Corp) or Microsoft Excel. In each case, I used a 5% level of significance.

## Chapter 3: Results

### 3.1 Diet of brown house snakes

I gathered 232 feeding records involving *B. capensis* (Table 3.1). Most prey remains found within museum specimens were mammal hairs. The validation of the HairSnap routine produced weak results (species level 46% of the time, genus-level 55% of the time, and family level 62% of the time) and thus able to allocate unknown samples to species, I have low confidence in them and have not used them as identifications in any subsequent analysis. The diet of *B. capensis* varied significantly across prey groups (One-way Chi-square test:  $X^2_{df=3} = 120.724$ ;  $P < 0.001$ ) with rodents being the predominant prey that accounted for approximately 47% of feeding records (Fig. 3.1). Reptiles also made up a considerable proportion of the overall diet (38%). I was able to confirm the presence of amphibians and birds within their diets of *B. capensis* but these only contributed 3% and 12% (respectively) to the overall diet. Overall, based on prey frequencies, I calculated Levins' measure of niche breadth for *B. capensis* as  $B = 2.63$ , which I standardized to  $B_A = 0.54$ .



**Figure 3.1: Percentages of prey types found within 232 feeding records of *Boaedon capensis*.**

Table 3.1: Prey items recorded during this study from the literature, using community science, and through the direct examination of dissected museum samples. Community science records sourced from Maritz & Maritz (2020). Museum voucher numbers reflect the catalogue ID numbers for the snakes from which the prey was identified. TM = Ditsong National Museum of Natural History (Tshwane); PEM-R = Bayworld (Port Elizabeth); TGE T = TG Eimermacher samples housed at McGregor Museum (Kimberly).

Class	Family	Taxon	Number of records	% of all records	Source
<b>Mammals</b>			<b>109</b>	<b>46.98</b>	
	<b>Muridae</b>		<b>32</b>	<b>13.79</b>	
		<i>Aethomys chrysophilus</i>	1		Maritz & Maritz 2020
		<i>Aethomys</i> sp.	2		TM 82352; PEM-R15475
		<i>Gerbilliscus afra</i>	2		TGE T10-58; TM 75085
		<i>Gerbilliscus leucogaster</i>	1		Maritz & Maritz 2020
		<i>Gerbillurus paeba</i>	1		PEM-R11349
		<i>Mastomys</i> sp.	1		PEM-R13817
		<i>Mus minutoides</i>	1		Jacobsen 1989
		<i>Mus</i> sp.	1		Hewitt & Power 1913
		<i>Mus triton</i>	1		Broadley 1966
		<i>Rhabdomys</i> sp.	3		PEM-R19819; PEM-R20; TGE T11-78
		<i>Rattus rattus</i>	4		Hewitt & Power 1913; Maritz & Maritz 2020
		<i>Rattus</i> sp.	3		Broadley 1966; Broadley 1983; Maritz & Maritz 2020
		Unknown murid	11		Fitzsimmons 1912; Hewitt & Power 1913; Broadley 1966; Maritz & Maritz 2020
	<b>Nesomyidae</b>		<b>1</b>	<b>0.43</b>	
		<i>Steatomys</i> sp.	1		Jacobsen 1989
	<b>Soricidae</b>		<b>4</b>	<b>1.72</b>	
		<i>Crucidura</i> sp.	1		PEM-R15475
		<i>Myosorex</i> sp.	1		TM 75088

	<i>Suncus</i> sp.	1	De Waal 1978
	Unknown shrew	1	Fitzsimons 1962
<b>Erinaceidae</b>		<b>1</b>	<b>0.43</b>
	<i>Atelerix frontalis</i>	1	Maritz & Maritz 2020
<b>Vespertilionidae</b>		<b>5</b>	<b>2.16</b>
	<i>Neoromicia capensis</i>	2	De Waal 1978; Van Wyk & Rautenbach 2005
	<i>Scotophilus dinganii</i>	2	Maritz & Maritz 2020
	Unknown vespertilionid	1	Maritz & Maritz 2020
<b>Molossidae</b>		<b>2</b>	<b>0.86</b>
	Unknown molossid	2	Maritz & Maritz 2020
<b>Other</b>		<b>64</b>	<b>27.59</b>
	Unknown bat	2	Maritz & Maritz 2020
	Unknown rodent	2	Fitzsimons 1962; Bruton & Haacke 1980;
	Unknown mammal	60	PEM-R1475; PEM-R11249; PEM-R11422; PEM-R11534; PEM-R12074; PEM-R13224; PEM-R13369; PEM-R13675; PEM-R13817; PEM-R15477; PEM-R15478; PEM-R154801; PEM-R16955; PEM-R19138; PEM-R19521; PEM-R21056; PEM-R21709; PEM-R15479; TGE T1-34; TGE T3-55; TGE T3-57; TGE T3-66; TGE T3-68; TGE T3-72; TGE T6-1; TGE T10-25; TGE T10-58; TGE T10-74; TGE T11-56; TGE T11-78; TM 14712; TM 16224; TM 21644; TM 29927; TM 32728; TM 41788; TM 47353; TM 47659; TM 47809; TM 47969; TM 47978; TM 48149; TM 51330; TM 54725; TM 573561; TM 64709; TM 64715; TM 64873; TM 69325; TM 73104; TM 75076; TM 75077; TM 75090; TM 80528; TM 805641; TM 82352; TM 82931; TM 84748; TM 84994; TM 85319
<b>Reptiles</b>		<b>88</b>	<b>37.93</b>
<b>Agamidae</b>		<b>18</b>	<b>7.76</b>
	<i>Agama aculeata</i>	1	Maritz & Maritz 2020
	<i>Agama atra</i>	5	De Waal 1978; Maritz & Maritz 2020
	<i>Acanthocercus atricollis</i>	12	Maritz & Maritz 2020
<b>Cordylidae</b>		<b>1</b>	<b>0.43</b>
	<i>Cordylus vittifer</i>	1	Jacobsen 1989
<b>Gekkonidae</b>		<b>38</b>	<b>16.38</b>
	<i>Afrogecko porphyreus</i>	1	Maritz & Maritz 2020

<i>Chondrodactylus bibronii</i>	2	Maritz & Maritz 2020
<i>Chondrodactylus turneri</i>	9	Broadley 1966; Maritz & Maritz 2020; TM 27265
<i>Hemidactylus mabouia</i>	7	Maritz & Maritz 2020; PEM-R 21798
<i>Hemidactylus mercatorius</i>	1	Loveridge 1953
<i>Hemidactylus platycephalus</i>	2	Maritz & Maritz 2020
<i>Hemidactylus</i> sp.	1	Broadley 1966
<i>Homopholis</i> sp.	2	TM 6136; TM 69655
<i>Homopholis walbergii</i>	2	Maritz & Maritz 2020; TM 76050
<i>Lygodactylus capensis</i>	2	Maritz & Maritz 2020
<i>Pachydactylus affinis</i>	1	Maritz & Maritz 2020
<i>Pachydactylus capensis</i>	3	De Waal 1978; Perry & Fisher 2006
<i>Pachydactylus mariquensis</i>	1	Branch and Braack 1987
<i>Pachydactylus</i> sp.	1	Broadley 1967
Unknown gecko	3	Maritz & Maritz 2020; TM 76052; TM 85318
<b>Scincidae</b>	<b>24</b>	<b>10.34</b>
<i>Mochlus sundevallii</i>	1	Jacobsen 1989
<i>Trachylepis capensis</i>	2	Hewitt & Power 1913; PEM-R 11434
<i>Trachylepis margaritifera</i>	1	Maritz & Maritz 2020
<i>Trachylepis punctatissima</i>	5	De Waal 1978; Maritz & Maritz 2020
<i>Trachylepis striata</i>	8	Broadley 1966; Maritz & Maritz 2020; TM 83974
<i>Trachylepis varia</i>	3	Jacobsen 1977
<i>Trachylepis wahlbergii</i>	1	Maritz & Maritz 2020
<i>Trachylepis</i> sp.	2	Maritz & Maritz 2020; TM 75073
Unknown skink	1	Fitzsimons 1962
<b>Lacertidae</b>	<b>2</b>	<b>0.86</b>
<i>Nucras holubi</i>	1	De Waal 1978
<i>Pedioplanis lineocellata</i>	1	Branch & Braack 1987
<b>Other</b>	<b>3</b>	<b>1.29</b>
Unknown lizard	2	Bruton & Haacke 1980; Maritz & Maritz 2020

	Unknown snake	1		Jacobsen 1989
<b>Colubridae</b>		<b>1</b>	<b>0.43</b>	
	<i>Dasypeltis scabra</i>	1		Maritz & Maritz 2020
<b>Typhlopidae</b>		<b>1</b>	<b>0.43</b>	
	<i>Rhinotyphlops lalandei</i>	1		Branch & Braack 1987
<b>Birds</b>		<b>28</b>	<b>12.07</b>	
<b>Columbidae</b>		<b>1</b>	<b>0.43</b>	
	<i>Streptopelia senegalensis</i>	1		Maritz & Maritz 2020
<b>Psittaculidae</b>		<b>1</b>	<b>0.43</b>	
	<i>Agapornis</i> sp.	1		Maritz & Maritz 2020
<b>Muscicapidae</b>		<b>1</b>	<b>0.43</b>	
	<i>Cercomela familiaris</i>	1		Maritz & Maritz 2020
<b>Meropidae</b>		<b>1</b>	<b>0.43</b>	
	<i>Merops bullockoides</i>	1		Maritz & Maritz 2020
<b>Motacillidae</b>		<b>1</b>	<b>0.43</b>	
	<i>Motacilla aguimp</i>	1		Maritz & Maritz 2020
<b>Passeridae</b>		<b>7</b>	<b>3.02</b>	
	<i>Passer diffusus</i>	1		Maritz & Maritz 2020
	<i>Passer domesticus</i>	3		Maritz & Maritz 2020
	<i>Passer melanurus</i>	1		Maritz & Maritz 2020
	<i>Passer</i> sp.	2		Maritz & Maritz 2020
<b>Ploceidae</b>		<b>8</b>	<b>3.45</b>	
	<i>Ploceus</i> sp.	3		Maritz & Maritz 2020
	<i>Ploceus capensis</i>	2		Maritz & Maritz 2020
	<i>Ploceus intermedius</i>	3		Maritz & Maritz 2020
<b>Pycnonotidae</b>		<b>1</b>	<b>0.43</b>	
	<i>Pycnonotus tricolor</i>	1		Maritz & Maritz 2020
<b>Estrildidae</b>		<b>3</b>	<b>1.29</b>	
	<i>Estrilda astrild</i>	2		Hockey et al. 2005
	<i>Spermestes nigriceps</i>	1		Jackson 2016

<b>Other</b>		<b>4</b>	<b>1.72</b>	
	Unknown birds	4		Fitzsimmons 1962; Maritz & Maritz 2020
<b>Amphibians</b>		<b>7</b>	<b>3.02</b>	
<b>Pyxicephalidae</b>		<b>5</b>	<b>2.16</b>	
	<i>Amietia delalandii</i>	2		Maritz & Maritz 2020
	<i>Amietia fuscigula</i>	1		Maritz & Maritz 2020
	<i>Tomopterna</i> sp.	2		Maritz & Maritz 2020
<b>Other</b>		<b>2</b>	<b>0.86</b>	
	Unknown amphibian	2		Broadley 1966
<b>Total</b>		<b>232</b>	<b>100</b>	



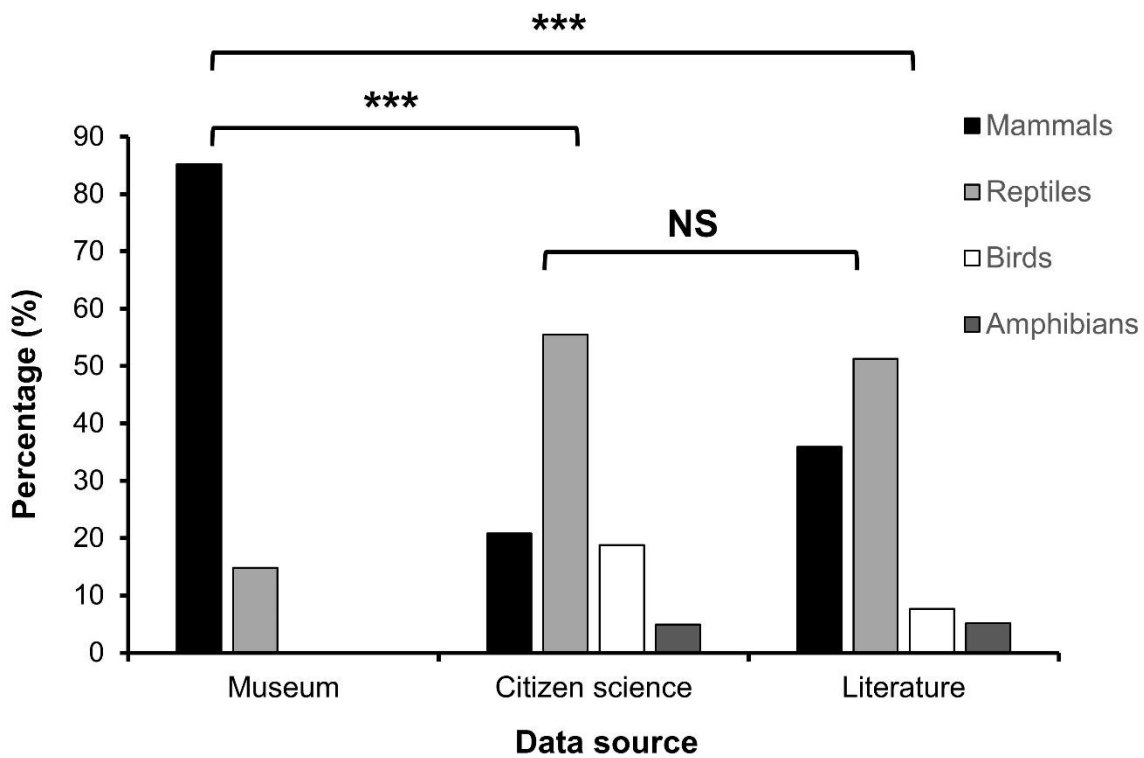


Table 3.2: Replicates of training data set that included the number of individuals from which hair was taken and accuracy of the identification for hair impressions.

Taxon	No. individuals	No. slides	% correctly identified
Emballonuridae	1	23	50
<i>Taphozous</i>	1	23	50
<i>Taphozous mauritanus</i>	1	23	50
Muridae	26+	251	62
<i>Acomys</i>	Unknown	8	100
<i>Acomys subspinosus</i>	Unknown	8	100
<i>Aethomys</i>	2	77	43
<i>Aethomys namaquensis</i>	2	63	66
<i>Aethomys</i> sp.	2	77	29
<i>Gerbilliscus</i>			
<i>Gerbilliscus afra</i>	Unknown	39	50
<i>Gerbilliscus</i> sp.	2	12	100
<i>Gerbilliscus paeba</i>	2	101	30
<i>Otomys</i>	Unknown	35	66
<i>Otomys irroratus</i>	Unknown	35	50
<i>Mastomys</i>	1	53	60
<i>Mastomys natalensis</i>	Unknown	16	50
<i>Mastomys</i> sp.	1	37	50
<i>Mus</i>	4	99	50
<i>Mus</i> sp.	1	31	33
<i>Mus minutoides</i>	2	31	33
<i>Mus musculus</i>	1	37	25
<i>Myotomys</i>	Unknown	31	66
<i>Myotomys unisulcatus</i>	Unknown	31	25
<i>Parotomys</i>	Unknown	11	0
<i>Parotomys</i> sp.	Unknown	11	0
<i>Rhabdomys</i>	4	95	70
<i>Rhabdomys pumilio</i>	1	18	100
<i>Rhabdomys</i> sp.	3	77	50
<i>Rattus</i>	1	30	66
<i>Rattus rattus</i>	1	30	66
Hipposideridae	4+	90	86
<i>Hipposideros</i>	Unknown	28	33

	<i>Hipposideros caffer</i>	Unknown	28	33
		Unknown	152	53
Miniopteridae		Unknown	13	70
	<i>Miniopterus</i>	Unknown	26	66
	<i>Miniopterus natalensis</i>	Unknown	26	66
Molossidae		1	26	65
	<i>Tadarida</i>	1	52	60
	<i>Tadarida aegypticus</i>	1	52	25
Nesomyidae		Unknown	33	52
	<i>Dendromus</i>	Unknown	26	50
	<i>Dendromus melanotis</i>	Unknown	26	33
	<i>Saccostomus</i>	Unknown	28	33
	<i>Saccostomus campestris</i>	Unknown	28	33
	<i>Steatomys</i>	Unknown	12	100
	<i>Steatomys krebsii</i>	Unknown	12	50
Nycteridae		1	20	58
	<i>Nycteris</i>	1	41	50
	<i>Nycteris thebaica</i>	1	41	25
Pteropodidae		1	30	55
	<i>Eidolon</i>	1	61	50
	<i>Eidolon helvum</i>	1	61	66
Rhinolophidae		1	8	0
	<i>Rhinolophus</i>	1	19	0
	<i>Rhinolophus clivosus</i>	1	19	0
Soricidae		2	24	64
	<i>Crocidura</i>	1	24	33
	<i>Crocidura</i> sp.	1	24	33
	<i>Myosorex</i>	1	23	100
	<i>Myosorex</i> sp.	1	23	100

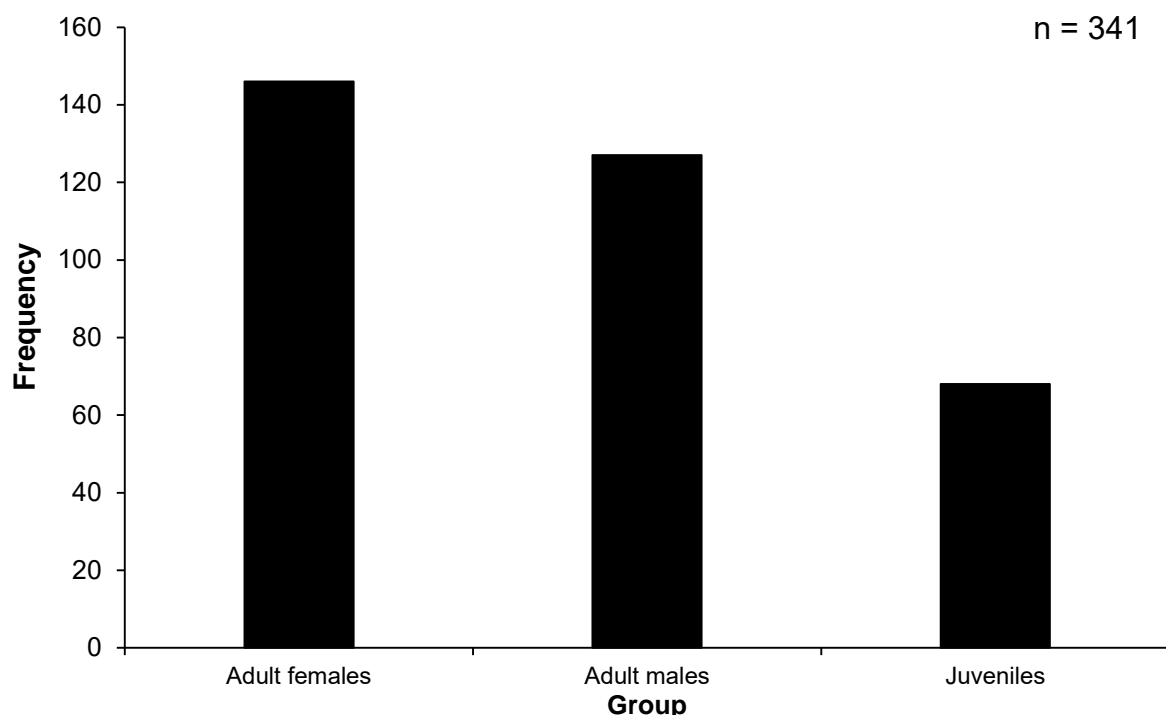
The majority of dietary data were collected from community science observations (as reported in Maritz & Maritz 2020) and dissections of museum specimens (53% and 31%, respectively). Prey items identified from museum sources consisted exclusively of mammals and squamate reptiles, whereas community science and literature sources additionally provided records of the consumption of amphibians and avian prey (Fig. 3.2). The proportional use of prey from museum sources differed significantly to community science observations ( $X^2_{df=3} = 86.71, P < 0.001$ ) and literature reports ( $X^2_{df=3} = 30.32, P < 0.001$ ). However, there was no difference in the proportional use of prey types between community science and literature sources ( $X^2_{df=3} = 5.50, P = 0.138$ ). Taken individually, the dietary niche of brown house snakes according to each source was  $B_A = 0.10, B_A = 0.52$ , and  $B_A = 0.41$  for museum data, community science observations, and literature reports respectively.



**Figure 3.2: Percentage of dietary records of different prey types for brown house snakes from three different sources. Statistical comparisons are Chi-square results (NS =  $P > 0.05$ , \*\*\* =  $P < 0.01$ ).**

### 3.2 Morphological correlates of diet

Of the 341 brown house snakes I measured, 273 of these were adults (80%) and 68 were juveniles (20%) (Figure 3.3). The ratio between adults and juveniles was therefore 4:1 in favor of adults (Chi-square test:  $X^2_{df=1} = 123.24$ ,  $P < 0.001$ ). Of the 273 adult snakes, 146 were female and 127 were male yielding no significant variation in the ratio between sexes in my sample (Chi-square test:  $X^2_{df=1} = 1.32$ ,  $P = 0.25$ ). The sexes of the juvenile snakes were not determined.



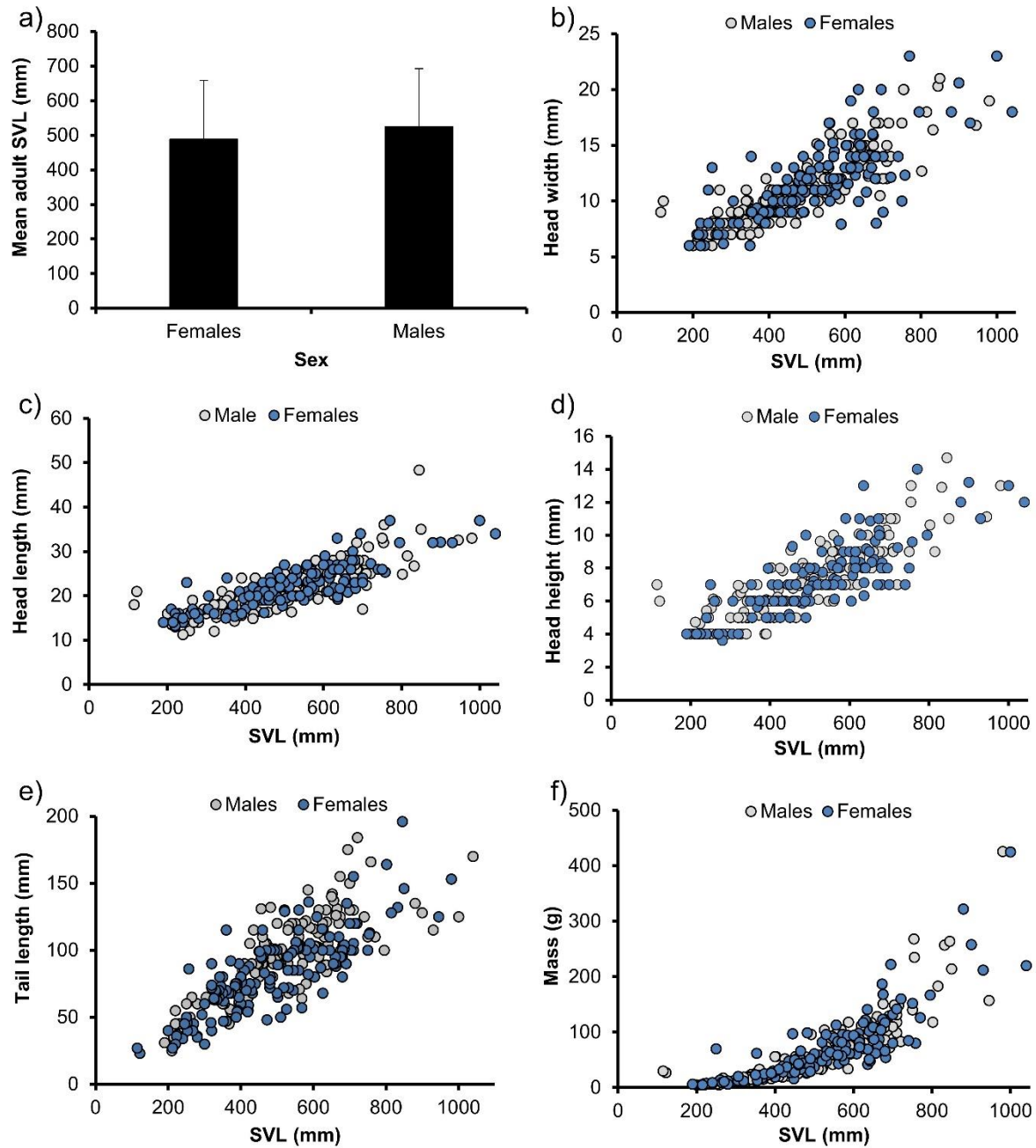
**Figure 3.3: Numbers of adult female, adult male, and unknown juvenile brown house snake specimens measured.**

One-way ANOVA and ANCOVA tests revealed that there were no significant differences in morphological traits between adult male and adult female brown house snakes (Table 3.3). Average SVL (males:  $487.84 \pm 170.68$  mm; females:  $524.65 \pm 168.32$  mm) did not differ between males and females (Figure 3.4a). Head sizes were also statistically similar across the two sexes when accounting for SVL (Figure 3.4b-d). As such, adult male and adult female

brown house snakes that had the same SVL therefore have the same or similar sized heads. Only tail length was significantly different (males:  $94.69 \pm 32.58$  mm; females:  $81.30 \pm 32.23$  mm) with adult males having longer tails on average (Figure 3.4e). Average body mass did not differ between sexes (Figure 3.4f).

Table 3.3: Results of ANOVA and ANCOVA tests comparing morphological traits of adult male and adult female brown house snakes. Significant effects shown in bold text.

Trait	Covariate	F	P	df
Snout-vent length	-	3.199	0.075	1, 271
Head length	SVL	1.582	0.210	1, 263
Head height	SVL	1.75	0.187	1, 261
Head width	SVL	0.057	0.811	1, 263
<b>Tail length</b>	<b>SVL</b>	<b>13.988</b>	<b>&lt; 0.001</b>	<b>1, 270</b>
Mass	SVL	0.558	0.456	1, 268



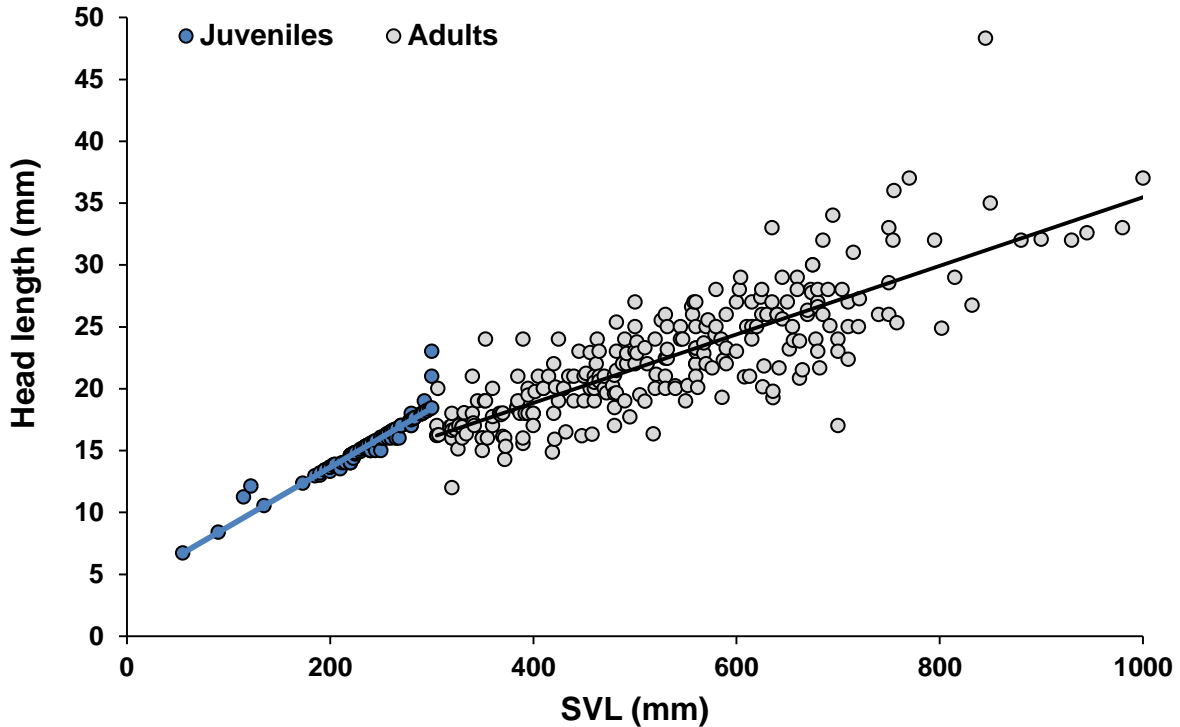
**Figure 3.4: Comparisons of morphological traits between adult male and adult female brown house snakes: a) mean SVL, b) head width, c) head length, d) head height, e) tail length, and f) mass.**

Adult and juvenile brown house snakes displayed obvious differences in absolute head size.

This trend remained present that adults have larger heads than juveniles (One-Way

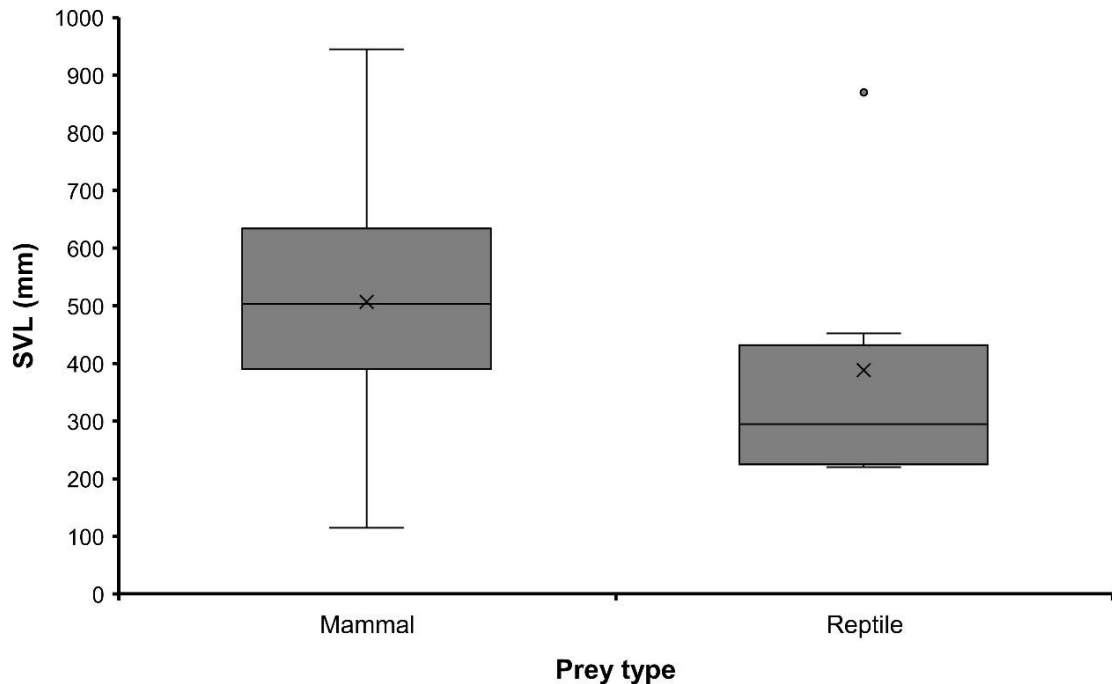


ANCOVA:  $F_{1, 321} = 13.170$ ,  $P < 0.001$ ). On average, the head lengths of adults were nearly double that of juveniles (Fig. 3.5).



**Figure 3.5: Head lengths relative to SVLs of adult and juvenile brown house snakes.**

Of the snakes for which I had body size measurements and feeding data ( $n = 84$ ), snakes that ate mammals ( $n = 72$ , mean  $\pm$  SD =  $506.65 \pm 166.76$  mm) had significantly larger SVL's (One-way ANOVA test:  $F_{1, 106} = 4.852$ ,  $P = 0.03$ ; Figure 3.6) than those that ate reptiles ( $n = 12$ ; mean  $\pm$  SD =  $388.17 \pm 239.16$  mm). Conversely, I found no evidence of differences in dietary preferences between sexes as there was no apparent association between sex and prey types consumed (Chi-square test:  $X^2_{df=1} = 0.114$ ,  $P = 0.736$ ).

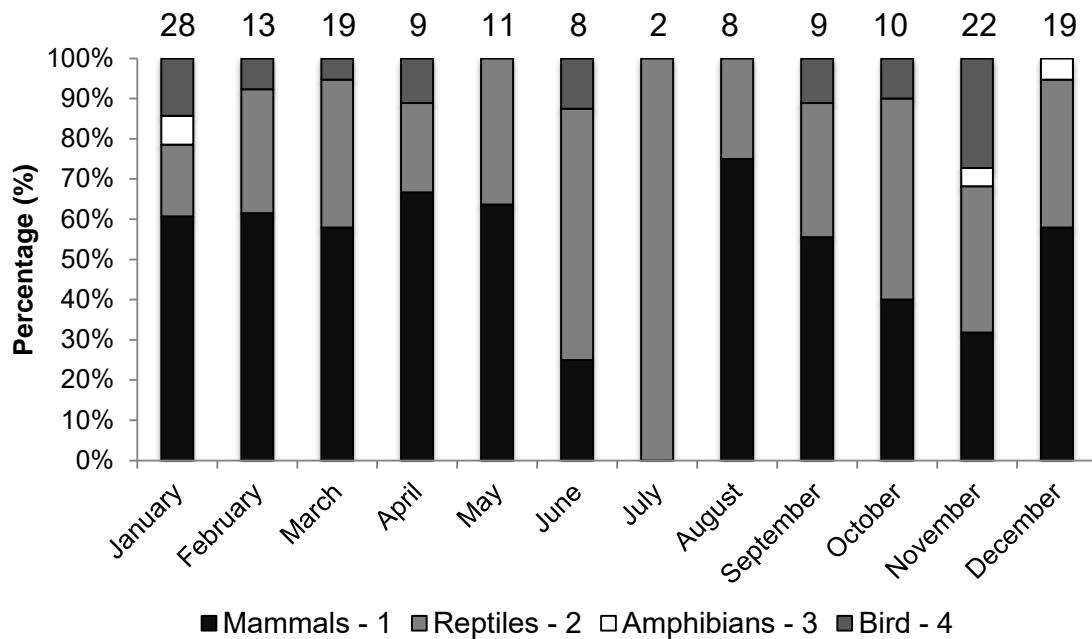


**Figure 3.6: Average and SD SVL of 84 museum specimen brown house snakes that had consumed mammalian vs reptilian prey (One-way ANOVA test:  $F_{1,106} = 4.852$ ,  $P = 0.03$ ).**

**The box represents the interquartile range, the middle line of the box represents the median value, and the x represents the mean value. The whiskers represent the minimum and maximum values of the range.**

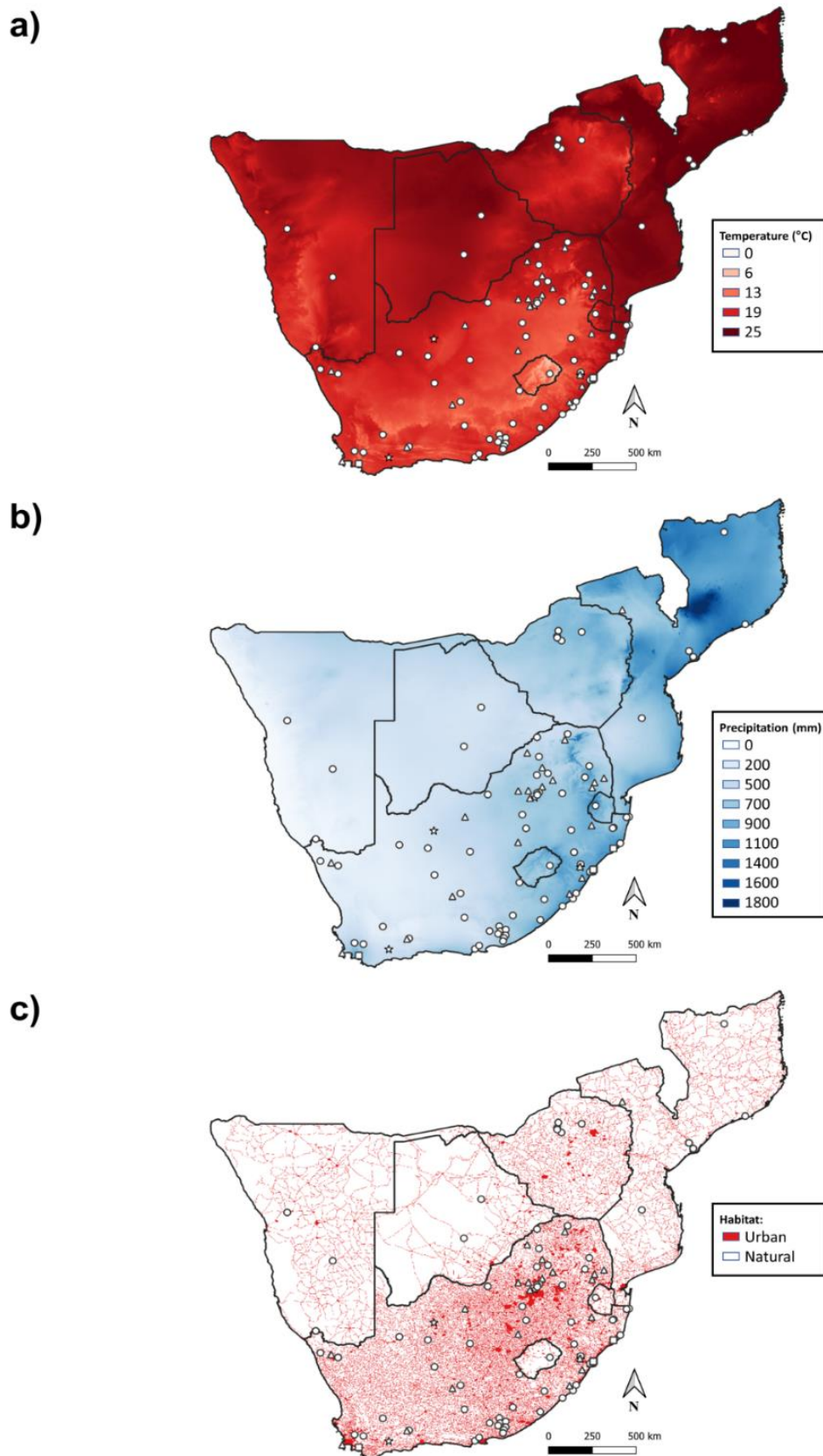
### 3.3 Ecological correlates of diet

Prey consumed by *B. capensis* was mostly similar each month. *B. capensis* feeds on mammalian prey items year-round but the proportions for the remaining prey types vary slightly per month (Figure 3.7). Although sample sizes were small in winter months, my data suggest the possibility that reptiles are predominantly preyed upon during winter months (June and July), and are more frequently utilized than amphibians and birds respectively. Birds and amphibians appear to be utilized to the same degree throughout the year.



**Figure 3.7: The prey items of *Boaedon capensis* for each month throughout the year. Sample sizes for each month are presented above each bar.**

I found no association present between climate and prey types consumed by *B. capensis*. Average temperature (ANOVA test:  $F_{3,110} = 0.641$ ,  $P = 0.59$ ; Figure 3.8a) and average precipitation (ANOVA test:  $F_{3,110} = 3.537$ ,  $P = 0.17$ ; Figure 3.8b) both did not affect which prey type was consumed by snakes. Additionally, there was no significant association between prey type and the combined effects of temperature and precipitation (MANOVA test:  $F_{6,218} = 1.86$ , Wilks Lambda = 0.904,  $P = 0.086$ ). Similarly, there was no significant difference in prey consumed between urban and natural habitats (Two way Chi-Square test:  $X^2_{df=6} = 6.01$ ,  $P = 0.423$ ; Figure 3.8c).



**Figure 3.8:** *Boaedon capensis* foraging events across southern Africa with relation to variation in a) temperature, b) precipitation, and c) land-use. The prey items are displayed as different shapes on the map: mammals (circles), reptiles (triangles), amphibians (squares) and birds (stars).

## Chapter 4: Discussion

My examination of the dietary composition of the brown house snake presents conclusive, empirical evidence that while these snakes predominantly eat rodents, they readily utilise prey from all four major tetrapod prey types (amphibians, birds, mammals, and reptiles).

Importantly, I demonstrate that there is a significant likelihood of an ontogenetic shift in diet between juveniles and adults. Adults possess 1.46 times longer heads than juveniles and are therefore less constrained in terms of gape size limitations in prey selection, and my results show that there was an apparent shift in dietary preferences associated increases in body size from small lizards to larger endothermic prey. However, this finding was potentially a result of poor representation of reptiles in museum specimens for which I had limited morphological data. Conversely, there were no apparent differences in morphology or diet between adult males and female snakes. Diet showed a demonstrable difference across data sources, with museum data being biased towards mammals and reptiles whereas community science also included amphibians and birds. Similarly, factors such as climate and land use (urban versus natural) also did not affect prey utilisation.

My findings show that the degree to which brown house snakes utilise small mammal prey has been overestimated in most previous literature. However, some prior descriptions of their diet from published books and field guides appear to be congruent with my results. Broadley (1990) states that brown house snakes mostly prey on rats, mice, and small rodents but also consume shrews, bats, birds, eggs, frogs, and other reptiles and that young snakes mostly eat skinks. This general pattern is similarly reported by Branch (1998), Alexander & Marais (2007), and Spawls et al. (2018), the former and latter of which claim that in dry or arid areas reptiles are the favoured prey. My findings also support the hypothesis that brown house snakes undergo an ontogenetic shift in diet from initially consuming small lizards to gradually including larger and more diverse prey as they mature as suggested by Branch



(1998) and Spawls et al. (2018). However, my results do not conform with their hypotheses regarding prey preferences in arid regions as I found no association between prey and temperature or precipitation.

Ontogenetic shifts in diet are not uncommon in snakes (Plummer 1984; Vincent et al. 2004; Vincent et al. 2007) and it is not surprising that this phenomenon is present in brown house snakes. However, my results here are somewhat limited given my small sample size of snakes with both prey and body measures. Overall, I only had 12 specimens that ate reptiles, however, two of those were of large adults. Moreover, several of the photographic predation records from citizen scientists appear to show adults consuming lizards, including large species like agamas (see Appendix Figure S1). Increased sampling could ultimately provide a clearer picture. However, ontogenetic shifts in diet have been documented for other southern African species such as vine snakes (*Thelotornis capensis*) fed exclusively on reptiles whereas large individuals fed on a variety of different prey types (Shine et al. 1996a). In North America, Durso & Mullin (2017) observed an ontogenetic shift from lizards and lizard eggs to turtle eggs and toads in hog-nosed snakes (*Heterodon nasicus*). Brown house snakes show a greater factorial increase in length from juveniles to adults in comparison (*Thelotornis capensis* = 16.02, *Heterodon nasicus* = 10.57, *Boaedon capensis* = 18.91), suggesting that there is likely to be an ontogenetic shift in their diets as well.

My analyses revealed little evidence of sexual size dimorphism in overall body size and head morphology in adult brown house snakes. Male and female brown house snakes of a similar SVL are likely to have similar head measures and are therefore similarly constrained in terms of gape size and ingestion ability. The lack of differences in feeding morphology between males and females suggests that the spectrum of prey available to both groups are likely to be the same (Cundall & Greene 2000). However, male snakes had significantly larger tails than females. Longer tails in males are typical in snakes (King et al. 1999), primarily as a result of



the requirement of males to house and accommodate hemipenes and retractor muscles (Clarke 1966; King 1989). Moreover, females tend to have short tails as a result of natural selection favouring increased reproductive capacity (Clarke 1966; King 1989). Additionally, the evolution of tail length in snakes may also be driven by ecological factors such as habitat use. Typically, arboreal snakes tend to have longer tails than terrestrial species (King 1989).

My data provide the first detailed examination of the potential for sexual size dimorphism in brown house snakes. Sexual size dimorphism is common in snakes (Camilleri & Shine 1990; Bonnet et al. 1998) and several studies have linked intersexual differences in morphology to differential prey utilisation between males and female snakes. *For example.*, Shine et al. (1998) found that horned adders (*Bitis caudalis*) in southern Africa exhibit distinct differences in diet between sexes whereby males with smaller heads predated greater proportions of ectothermic prey than females with larger heads who predominantly consumed endotherms. Pearson et al. (2002) found a similar pattern in carpet pythons (*Morelia spilota*) in Australia. However, intersexual divergences in diet may also occur within species that do not exhibit dimorphism in head size. Shine (1996b) found that coral snakes (*Aspidelaps scutatus*) showed significant divergence in prey use between males and females despite having similar head morphology and attributes those sex-mediated differences in activity time and locations.

Overall, I was only able to identify a relatively small proportion of prey (< 40%) to species level, largely owing to the difficulties associated with identifying rodents from hair remains. The identification of hair cuticle scale patterns is challenging for several reasons, most notably the requirement for a database of known patterns and the expertise required to prepare slides for analyses. Given the broad distribution of *B. capensis* across multiple countries and the large diversity of mammals that occurs throughout their range, my training dataset was likely too small to accurately estimate each sample to species level. It is unclear why known

samples did not always match with the training dataset. One possible reason could be the limited zoom range of my images. Foster et al. (2011) used images of hair cuticle scale patterns that ranged between 1000x to 2500x zoom whereas my images were limited to only 40x zoom. These differences in detail could potentially have impacted the accuracy of the plugin. Similar difficulties were encountered by Glaudas et al. (2017) during stomach content analysis of puff adders (*Bitis arietans*). Despite incorporating a machine learning approach, my attempts at identification were met with middling accuracy. Given that this approach was not overtly successful, future studies that seek to identify mammal remains from hair samples should seek to refine the techniques or employ alternative options. Consequently, we appear to currently be trapped in a situation in which hair remains are easy to detect in snake specimens but are not easy to identify. This challenge remains problematic and has severe implications for fine-scale dietary studies of snakes that primarily eat mammals (e.g. Greene 1983).

The discrepancies in the diet of brown house snakes as presented by different data sources shows a clear example of data bias and paints a misinformed picture of their dietary compositions when used in isolation. Traditional methods of collecting dietary records from examining the stomach contents of deceased specimens are limited in numerous ways. Firstly, digestion within the stomach results in prey items being destroyed or becoming increasingly unidentifiable. Additionally, easily digestible contents could result in a complete absence of evidence for consumption. As such, museum specimens tend to disproportionately contain mammal or reptile remains, a commonly occurring problem with snake dietary studies (see Glaudas et al. 2017; Layloo et al. 2017). Conversely, social media reports accounted for nearly all bird and amphibian records. However, social media reports suffer from a different form of bias in that they are almost always associated with anthropogenic influences. Fortunately, a growing recognition is being given to the fact that single-origin diet

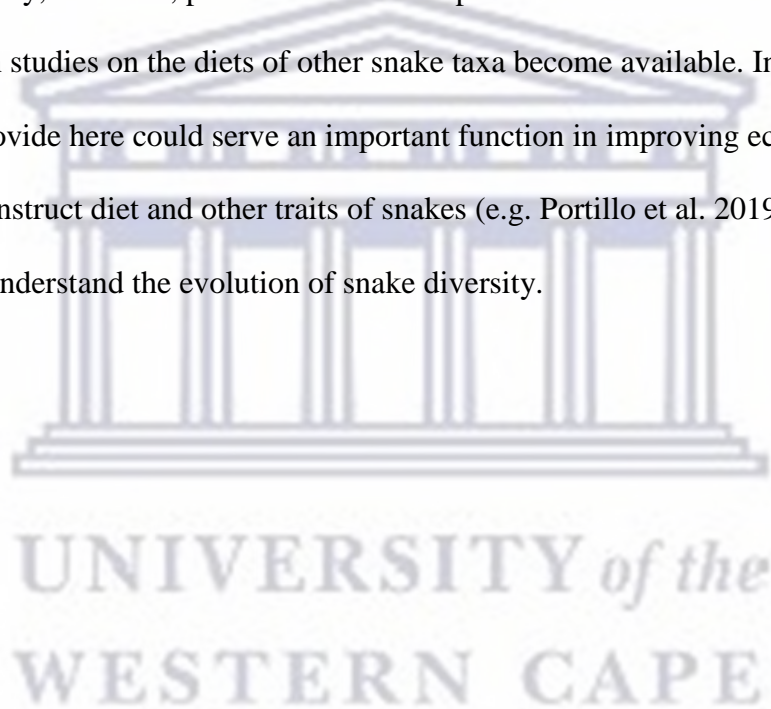
data can obscure variation in prey utilisation and niche breadth (Rodríguez-Robles 1998; Glaudas et al. 2017, Layloo et al. 2017, Maritz et al. 2020).

Another important facet to consider with regards to the diet of a species is geographical variation in prey utilisation. Differences in climate, geography, and habitat across a species range can influence the availability of different prey and therefore its diet can vary between populations. For example, populations of grass snakes (*Natrix natrix*) on mainland Italy consume different prey to populations on nearshore islands (Luiselli et al. 2005). Similarly, de Quiroz et al. (2001) found that different populations of Mexican garter snakes (*Thamnophis validus*) either ate mostly frogs or mostly fish depending on their location across the Pacific Coast of Mexico. However, although brown house snakes cover a considerable distribution range, I found no evidence of geographic variation in diet across southern African specimens, with temperature, precipitation, and land use seemingly having minimal effects on prey utilisation. However, my analyses were based on broad, aggregated classifications of prey classes (i.e., amphibians, birds, mammals, and reptiles) and fine-scale variation at the species level could potentially produce different results.

Although my findings suggest that brown house snakes do not solely rely on rodents for prey and could persist on a diet of other taxa, particularly so for juveniles, their preferred prey appears to be rodent species. As a result, these snakes have the potential to suppress numerically abundant mammalian pest species thus potentially providing a regulatory ecosystem service beneficial to humans. In the Florida Everglades, invasive Burmese pythons (*Python bivittatus*) seemingly control small mammal populations (Holbrook & Chesnes 2011) through top-down predation. To my knowledge, this phenomenon has not yet been empirically observed by a native southern African snake species, however, brown house snakes provide a highly likely candidate species to do so. Both Broadley (1990) and Alexander & Marais (2007) mention the propensity of these snakes to devour entire nests of

rodents in a single meal. In urban areas, brown house snakes maintain their diet of native mammals (e.g.: *Mus* or *Mastomys*) but also include invasive pest species such as those of the genus *Rattus*. In areas where brown house snakes are present at high densities, invasive rodents are thus unlikely to flourish.

The diets of many species of southern African snakes remains poorly catalogued. Dietary information for closely related taxa to *B. capensis* remain relatively scarce (Maritz & Maritz 2020, but see Akani et al. 2008) and little is known about the diets of other members of *Boaedon*. My study, therefore, provides a baseline upon which further investigations can build upon when studies on the diets of other snake taxa become available. In addition, the dietary data I provide here could serve an important function in improving ecological studies that seek to reconstruct diet and other traits of snakes (e.g. Portillo et al. 2019; Naik et al. 2020) to better understand the evolution of snake diversity.



## **Chapter 5: Main conclusion and limitations**

### **5.1 Sexual size dimorphism and ontogeny within *Boaedon capensis***

In quantifying body and head morphology of *B. capensis* specimens I learnt that sexual size dimorphism is not present within *B. capensis* but that there is scope for an ontogenetic shift in dietary composition between juveniles and adults because of the large differences in head size. Smaller individuals tend to feed more frequently on reptiles than on mammals but unfortunately, I did not have information on snake-size, prey-size relationships for individuals that ate birds and amphibians due to limitations within museum specimen sampling. The evidence suggests that gape size limitations influence prey preferences within these snakes as they grow.

### **5.2 Specialist or generalist predation**

Contrary to field guides, secondary and primary literature, I provided quantitative evidence that brown house snakes prey upon an assortment of species from four major tetrapod classes. I collated novel evidence of proof that birds and amphibians are included within their diets, as well as bats. These snakes appear to prefer to feed on rodents, but per Levins' measure of standardized niche breadth ( $B_A = 0.49$ ), this species would not be classified as strictly being specialist feeders.

### **5.3 Data biases and limitations**

Bias in data collection was unavoidable given the nature of the study. Dietary records of feeding events for snakes are reliant on unpredictable factors due to the secretive nature of snake foraging and ecology. Observations of feeding events are rare, even for common anthropogenic associated species such as *B. capensis*. Additionally, museum records are limited to those specimens that were killed with prey in their systems and are further limited



by the types of prey that can remain undigested for identification purposes. Literature records were also limited in that this species has not been the explicit focus of a dietary study that seeks to quantify and profile their prey. Although there are problems with diet data collection, this study had ample data presented to make a valid conclusion based on their *B. capensis* diet.

My identification process also suffered from biases and limitations. The machine learning approach taken to identify mammal prey based on hair cuticle scale patterns was entirely reliant on our training data set. While I sought to include as many representative samples from southern African mammals as possible, including bats, the sheer diversity of mammal species occurring sympatrically with *B. capensis* meant that many species were not represented within our training dataset. As a result, some of our identifications could only be made to the genus or family levels rather than to species. Moreover, the preparation and analyses of hair cuticle slides requires expensive and precise microscopes with high levels of magnification in order to effectively capture the unique patterns of each sample.

#### **5.4 Recommendations**

Quantifying the diets of species remains an important ecological tool that can facilitate our understanding of species natural histories and roles within ecosystems. For such studies on snakes, I would recommend that a similar approach to what was done here be applied. The use of multiple sources of dietary information should be employed as sources used in isolation can produce misleading results. The use of community science data from social media is a growing resource that continually accumulates more evidence of ecological interactions between predators and prey. This resource should not be overlooked for future, similar studies. Identification of prey should also seek to emulate our approach with regard to machine learning protocols. However, here I would recommend establishing an extensive



training dataset to ensure accuracy with identifications. Fortunately, several southern African mammals are already catalogued within the works of Keogh (1985) as well as more recent undertakings by organizations such as the Urban Caracal Project. These resources should be combined and expanded upon.

I would also suggest that researchers perform detailed analyses on closely related taxa to the brown house snake to provide an evolutionary context for how diet evolved in this relatively poorly understood lineage. More information is needed for many close relatives and a better understanding of the diversity and ecology of these snakes can only be achieved through extensive cataloguing of their traits and natural histories.



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## Appendices

Table S1: Unknown hair samples that were identified via machine learning with the HairSnap program. Museum voucher numbers reflect the catalogue ID numbers for the snakes from which the prey was identified. Note that these identifications have low confidence associated with them.

Family	HairSnap identification	Museum voucher number
<b>Emballonuridae</b>		
	<i>Taphozous mauritanus</i>	PEM-R13224
<b>Muridae</b>		
	<i>Acomys subspinosus</i>	PEM-R13369; TGE T1-34
	<i>Aethomys namaquensis</i>	TGE T3-55
	<i>Aethomys</i> sp.	TM 47978; PEM-R21709
	<i>Crocidura</i> sp.	PEM-R19138; TM 82352
	<i>Gerbilliscus afra</i>	PEM-R15479; PEM-R11534; TM 54725
	<i>Gerbilliscus</i> sp.	PEM-R19521; TM 47969; TM 64873; PEM-R15478; TM 82931
	<i>Gerbillurus paeba</i>	TM 805641; TM 73104; TM 80528
	<i>Mastomys natalensis</i>	TM 69325
	<i>Mastomys</i> sp.	TM 573561; PEM-R1475
	<i>Mus</i> sp.	TM 75077; TM 48149; PEM-R11249; PEM-R15477
	<i>Mus minutoides</i>	PEM-R13675
	<i>Mus musculus</i>	PEM-R11422
	<i>Myotomys unisulcatus</i>	PEM-R12074
	<i>Otomys irroratus</i>	TGE T10-74; TM 47659; TM 84994
	<i>Parotomys</i> sp.	TGE T11-56
	<i>Rattus rattus</i>	TM 75076; PEM-R13817; TM 47809; TM 51330; TM 64715
	<i>Rhabdomys pumilio</i>	TM 85319; TGE T3-72; TM 21644; PEM-R154801
	<i>Rhabdomys</i> sp.	TGE T3-57; TGE T6-1; TM 16224; TM 84748; TM 75090
<b>Hipposideridae</b>		
	<i>Hipposideros caffer</i>	TGE T3-66
<b>Miniopteridae</b>		
	<i>Miniopterus natalensis</i>	PEM-R16955
<b>Molossidae</b>		
	<i>Tadarida aegypticus</i>	PEM-R21056
<b>Nesomyidae</b>		
	<i>Dendromus melanotis</i>	TGE T10-58
	<i>Saccostomus campestris</i>	TM 29927
	<i>Steatomys krebsii</i>	TGE T11-78
<b>Nycteridae</b>		
	<i>Nycteris thebaica</i>	TM 32728
<b>Pteropodidae</b>		



<i>Eidolon helvum</i>	TGE T3-68
Rhinolophidae	
<i>Rhinolophus clivosus</i>	TM 14712
Soricidae	
<i>Crucidura</i> sp.	TM 41788
<i>Myosorex</i> sp.	TGE T10-25; TM 47353; TM 64709



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**Figure S1: Examples of community science reports of adult brown house snakes consuming reptile prey. Photos taken by a) Erika Barnard De Jager, b) Dmitrii Savelev-Dyer, c) Tyrone Ping, and d) Holly Goulding.**