Assessing the risk of non-native small mammals in the South African pet trade

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GENERAL ABSTRACT

Humans have introduced non-native small mammalian species for various purposes, including hunting, biological control, farming, fur markets, ornamental, and pet trade. The latter has been cited as one of the main invasion pathways for some small mammals through accidental escapes and intentional releases of pets. In addition, the pet trade has been cited as one of the major threats to biodiversity loss and human health through the spreading of zoonotic diseases. The trade of non-native pets is growing in South Africa, and this is of great concern as some of these species may become invasive should they escape or be released from captivity. There is also a lack of information regarding which non-native small mammalian species are sold in South Africa. As a result, two primary sources of trade (online and pet shops) were assessed to determine the extent of small mammal trade in South Africa. A list of the traded small mammalian species was compiled online and physical pet shops to determine which species pose an invasion risk and have potentially high impacts. Mitochondrial gene regions were used to assess the taxonomy and genetic diversity of 156 rodent specimens collected in the South African pet shops. We also determined if their genetic diversity follows a geographically correlated pattern.

A total of seven websites and 122 pet stores in South Africa were recorded, with 24 non-native small mammalian species traded. Three provinces, Gauteng, Western Cape and KwaZulu-Natal, had the highest number of websites and pet shops selling these species. Overall, online trade had more species diversity when compared with pet shops. Rodents and primates dominated the trade; however, the European rabbit *Oryctolagus cuniculus*, guinea pig *Cavia porcellus*, Norwegian rat *Rattus norvegicus* and house mouse *Mus musculus* were the most available species in both online and pet shops.

In terms of the potential impacts, traded small mammalian species were associated with both socio-economic and environmental impacts. Impacts on agricultural and animal production (livestock) prevailed for the socio-economic category, while the impacts on animals (predation) and competition were the main mechanisms in the environmental impacts. Of the species recorded, 14 had potential climatic suitability; however, species such as Guinea pig *Cavia porcellus*, sugar glider *Petaurus breviceps*, domesticated ferret *Mustela putorius furo*, *M*. *musculus*, *O*. *cuniculus*, European grey squirrel *Sciurus carolinensis*, and *R*. *norvegicus* are likely to become invasive given their popularity in the trade, large climatic suitability, and history of invasion through releases and accidental escapes.

A total of 156 rodent samples were identified using molecular analyses, with 115 specimens identified as *M*. *musculus*, 35 as *R*. *norvegicus* and six as Southern multimammate mouse *Mastomys coucha*. Phylogenetic trees showed that the three species were monophyletic, and there was a genetic diversity within *M*. *musculus* and *R*. *norvegicus*. The specimens for *M*. *musculus* and *R*. *norvegicus* were more geographically diverse when compared with the specimens for *M*. *coucha*. As a result, this suggests that most of the provinces comply with the trade regulations as native species are prohibited from trade. The combined data recovered 19 unique haplotypes for *M*. *musculus* and eight haplotypes for *R*. *norvegicus*. However, the genetic diversity for *M*. *musculus* did not show a clear geographical pattern, while *R*. *norvegicus* showed a subtle geographic structure. Unique haplotypes in these species may be explained by the desire to breed rare varieties or introduce new strains from different pet trade sources. In conclusion, small mammalian species with high trade volume, suitable climate, potential environmental and socio-economic impacts are likely to become invasive and cause impacts in South Africa. In addition, *M*. *musculus* and *R*. *norvegicus* individuals may establish feral populations if released from captivity, given that their haplotypes were unique. Therefore, it is recommended to further monitor the pet trade (both online and physical pet shops), including surveillance, to determine if there are any escapes and releases from the trade.

PREFACE

The data described in this thesis were collected in all the nine provinces of South Africa from September 2018 to September 2019. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under Professor Colleen T. Downs and Dr Sandi Willows-Munro's supervision.

This thesis, submitted for the degree of Doctorate of Philosophy in Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, 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.

Signe [redacted]

Ndivhuwo Shivambu
April 2021

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

[redacted]

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Professor Colleen T. Downs

Supervisor

April 2021

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DECLARATION 1 - PLAGIARISM

I, Ndivhuwo Shivambu, 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 Management of Biological Invasion

Non-native small mammal species in the South African pet trade

Ndivhuwo Shivambu, Tinyiko C. Shivambu and Colleen T. Downs

Author contributions: NS and TCS conceived paper with CTD. NS and TCS collected and analysed the data, NS wrote the paper. TCS and CTD contributed valuable comments to the manuscript.

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A survey of non-native small mammals traded in South Africa: Pet shop owners' perceptions

Ndivhuwo Shivambu, Tinyiko C. Shivambu and Colleen T. Downs

Author contributions: NS and TCS conceived paper with CTD. NS and TCS collected and analysed the data, NS wrote the paper. TCS and CTD contributed valuable comments to the manuscript.

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Author contributions: NS and TCS conceived paper with CTD. NS and TCS collected and analysed the data, NS wrote the paper. TCS and CTD contributed valuable comments to the manuscript.

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Publication 5: Formatted for Mammalian Biology

Genetic diversity of non-native small mammal species sold in the South African pet shops

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Author contributions: NS conceived paper with SW and CTD. NS and TCS collected data, NS, SW and TCS analysed data, NS wrote the paper. TCS, SW and CTD contributed valuable comments to the manuscript.

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CHAPTER 1

General introduction

1.1 Introduction

1.1.1 Biological invasions

Biological invasions are a major threat to biodiversity loss, economies and human health (Hall 2010; Mačić et al. 2018; Gallardo et al. 2019). Biological invasions occur when non-native species establish self-sustaining populations and spread in areas outside their natural ranges (Richardson et al. 2003; Mačić et al. 2018). When these species establish, reproduce rapidly, and cause adverse environmental and/or socio-economic impacts, they are called invasive non-native/exotic or alien species (Williamson and Fitter 1996; Keller et al. 2011; Selge et al. 2011; Gallardo et al. 2019). In the field of biological invasions, species occurring outside their natural distribution ranges are called "non-native", "alien", "exotic", "introduced", "foreign", or "non-indigenous" (Occhipinti-Ambrogi and Galil 2004; Falk-Petersen et al. 2006). In most cases, these species might survive, subsequently, reproduce and disperse by means of natural dispersal or human activities (Occhipinti-Ambrogi and Galil 2004; Falk-Petersen et al. 2006).

1.1.2 Invasion pathways

Non-native species have to overcome a series of barriers before becoming invasive (Blackburn et al. 2011). These stages are explained in Blackburn et al. (2011), and they include transport, introduction, establishment and spread. Non-native species are introduced through two broad categories, i.e accidental and intentional introduction (Frenot et al. 2005; Hulme 2009; Measey et al. 2017). The accidental introduction includes the transportation of species through ballast water, as stowaway or hitchhikers (attached to ships or aeroplanes), and contaminants of transported goods through human activities such as trade and travel (Hulme 2009; Faulkner et al. 2016). The intentional pathway includes the introduction of species directly into the environment (e.g. biological control, medicinal, hunting, fishing, and aesthetics) and introductions via captivity (e.g. horticulture, zoos, research, and pet trade) (Martin and Coetzee 2011; Britton and Orsi 2012; Faulkner et al. 2016; Carpio et al. 2020). Of the intentional pathways, the pet trade has received a lot of attention over the recent years as the global trade in live animals has increased and as it contributes to species invasions and biodiversity loss (Keller and Lodge 2007; Ng et al. 2016; Symes et al. 2018; Lockwood et al. 2019).

1.1.3 Pet trade as an invasion pathway

The trade of non-native species as pets or companion animals is increasing, and it involves a variety of species, from birds, fishes, gastropods, invertebrates, reptiles and mammals (van Wilgen et al. 2010; Su et al. 2016; Chucholl and Wendler 2017; Maligana et al. 2020; Shivambu et al. 2020a, b; Nelufule et al. 2020). Fish, reptiles, and birds dominate the pet trade industry, followed by amphibians and mammals (Bush et al. 2014; D'Cruze and MacDonald 2016; Green et al. 2020; Gippet and Bertelsmeier 2021). In the mammalian group, rodents, primates and rabbits are amongst the most traded groups for research and pet trade (Ellis and Mori 2001; Grant et al. 2017; Carpio et al. 2020). The increase in the demand for small mammal pets can be explained by the fact that they are generally cheap to care for or maintain, easy to breed in captivity and are relatively cheap to purchase (Quesenberry and Carpenter 2011; Sirois 2016). Celebrities have also influenced the keeping of non-native small mammals. For example, many people in the United States of America (USA) became interested in kinkajou *Potos flavus* after its appearance with a well-known celebrity, Paris Hilton, in 2007, and this has increased its popularity in the USA (Harrington et al. 2019). In the United Kingdom, it has been reported that celebrities prefer to keep domesticated ferrets *Mustela putorius furo* as pets, and this may have increased their popularity in the country where about 800,000 ferrets are known to be kept as pets (Bament 2013).

Keeping non-native pets comes with a lot of responsibilities; most of these pets require exceptional care, including medication, proper housing, and specialised diets, some of which are expensive (Grant et al. 2017; Harrington et al. 2019). Unfortunately, when some of the people could no longer afford to provide for their expensive pets or when the interest in keeping an exotic pet fades, they abandon them to the wild (Reaser and Meyers 2007; Stringham and Lockwood 2018). Other reasons why pet animals are released into the wild include species growing into large sizes, aggressive temperaments, humane treatment, high reproductive rates and fear of zoonotic disease transmission (Padilla and Williams 2004; Reaser and Meyers 2007; Secretariat of the CBD 2010; Stringham and Lockwood 2018). The trade of non-native pets poses an invasion risk, as several invasive species have established feral populations through this way (Keller and Lodge 2007; Gaertner et al. 2015; da Rosa et al. 2017).

Captive species can only become invasive or feral if they accidentally escape or are intentionally released into the environment. Feral species refers to animals that were domesticated but now live in the wild, sometimes causing environmental and socio-economic impacts (Marbuah et al. 2014; Décory 2019). For example, the domesticated cat *Felis catus* is regarded as one of the world's worst invasive species cited to negatively impact biodiversity through competition, predation, disease and hybridisation (Lowe et al. 2000; Trouwborst et al. 2020). The Gambian pouched rat *Cricetomys gambianus,* which became invasive after being released by a breeder in southern Florida, is considered as a new threat to native and endemic animals such as the Largo cotton deer mouse *Peromyscus gossypinus allapt* and Largo woodrat *Neotoma floridana smalli* (Perry et al. 2006).

1.1.4 Sources of trade

Non-native pets can be sourced from the breeders, the wild, rescue clubs, laboratories, pet shops and online (Stoakes et al. 2014; Maligana et al. 2020; Shivambu et al. 2020a). In general, online /the internet trade has been indicated to offer a variety of taxa, including endangered, potentially invasive, and protected species (Derraik and Phillips 2010; Daut et al. 2015; Faulkes 2018; Siriwat and Nijman 2018; Shivambu et al. 2020b). Most of the non-native species are commonly sold by their common names and not scientific names in the pet trade industry (Lankau et al. 2017; Maligana et al. 2020; Nelufule et al. 2020; Shivambu et al. 2020b). There are also taxonomic uncertainties on the traded species sourced from both online and pet shops (Maligana et al. 2020; Nelufule et al. 2020; Shivambu et al. 2020b). The taxonomy of closely related or cryptic species are generally confused in the pet trade industry; for example, Shivambu et al. (2020b) found that only 13 out of 36 tarantulas were correctly identified, while Nelufule et al. (2020) found that all the snails sold as *Achatina immaculata* were in fact *Achatina fulica*. In addition, molecular analyses have been used to identify the origin of traded species such as *P. breviceps* and pangolins *Manis* spp. (Zhang et al. 2015; Campbell et al. 2019). Consequently, taxonomic uncertainty limits the ability to trace the source of trade, access the actual distribution of species in the pet trade industry and determine the invasion impact of a traded species (Strecker et al. 2011; Ng et al. 2016).

1.1.5 Impacts associated with the pet trade

In the current Anthropocene era, the wildlife trade is cited as a major cause of several species decline (Symes et al. 2018a, b; Morton et al. 2021). This is of great concern as threatened species are also traded as pets and may therefore go extinct as a result of the trade (Flecks et al. 2012; Raghavan et al. 2013; Siriwat and Nijman 2018; Frank and Wilcove 2019). Although the pet trade has not been linked to the extinction of species, it has been implicated in the decline of some species. For example, the population of Macaw *Ara* spp is said to may have declined by at least 70% in the last 50 years (Herrera and Hennessey 2007). Again, the populations of green python *Morelia viridis* and cotton-top tamarin *Saguinus oedipus* have declined as a result of the illegal pet trade (Savage et al. 2010; Lyons and Natusch 2011).

Some of the traded species may accidentally escape or be released from captivity and cause environmental and socio-economic impacts (Marbuah et al. 2014; Su et al. 2015; Shivambu et al. 2020c). Once these species colonise a habitat, they may dislocate native animals through competition, disease transmission, predation, hybridisation, altering ecosystem processes, herbivory or grazing and dispersing seeds of non-native vegetation (Charles and Dukes 2008; Blackburn et al. 2014; Linders et al. 2019). Invasive small mammals such as sugar glider *Petaurus breviceps*, black tufted-ear marmoset *Callithrix penicillata*, and *M. putorius furo* have negatively impacted biodiversity by preying on native species (Stojanovic et al. 2017; Campbell et al. 2018). Some of the invasive small mammal species hybridise with native species. As a result, they negatively affect their population genetic pool; for example, the common marmoset *Callithrix jacchus* hybridise with vulnerable buffy-tufted marmosets *C. aurita* in Brazil (Nogueira et al. 2011; Malukiewicz et al. 2014). In addition, the eastern grey squirrel *Sciuris carolinensis* has been linked to the decline of red squirrels *S. vulgaris* through transmitting parapoxvirus disease in the UK (Rushton et al. 2000; Sainsbury et al. 2000).

Both domesticated and wild animals can spread diseases to humans and other animals (Chomel et al. 2007; Grant et al. 2017). *Mustela putorius furo* have been implicated in transmitting *Bovine tuberculosis* to livestock in New Zealand (Byrom 2002). Outbreaks of diseases such as Lymphocytic choriomeningitis and Seoul virus in the USA have been linked to pet rodents (Childs et al. 2019). Most of these diseases are spread through petting, physical contact, bites, scratches, exposure to excreta or saliva (Wolfs et al. 2002; Gaastra et al. 2009; Hönlinger et al. 2005; Halsby et al. 2017). Other socio-economic impacts include damage of gardens, orchards, agricultural importance crops, and infrastructures such as roof voids, telephone and electric wires (Signorile and Evans 2007; Merrick et al. 2016). In addition, the European rabbit *Oryctolagus cuniculus* has been reported to negatively impact agricultural production through competition with livestock for pastures in New South Wales, Australia (Fleming et al. 2002).

1.1.6 Impact assessment

Although the negative impacts associated with non-native pets are known in many countries, the demand for non-native pets continues to grow (Bush et al. 2014; Moorhouse et al. 2017). In South Africa, van Wilgen et al. (2008) indicated that the National Environmental Management: Biodiversity Act (No. 10 of 2004) (NEM: BA) requires that a risk assessment be conducted before a permit may be issued for activities involving the non-native pet trade. To keep an ecosystem free of invasive non-native animals, preventing the introduction, release or escape of captive animals is the best method (Mazzotti et al. 2015). To date, impact and risk assessment protocols are one of the best and cost-effective methods in identifying which species should be prevented and have been used for different taxa, including introduced, non-introduced, established feral and invasive species (Fujisaki et al. 2010; Kumschick and Nentwig 2010; Kumschick and Richardson 2013; Patoka et al. 2014; Marr et al. 2017; da Rosa et al. 2017; Hagen and Kumschick 2018; Weiperth et al. 2018; Shivambu et al. 2020c). In addition, impact assessment protocols can be used together with the species distribution modelling as a rapid screening tool to determine areas that will be likely invaded or impacted by introduced or invasive species (Kitzberger et al. 2000; Thuiller et al. 2004; Giovanelli et al. 2008; Shivambu et al. 2020c).

1.1.7 Pet trade in South Africa

Several non-native pet or ornamental species have become invasive through accidental escapes in South Africa, for example, the rose-ringed parakeet *Psittacula krameri*, *F. catus*, and *S. carolinensis* (Measey et al. 2020; Shivambu et al. 2020c). There is, however, a growing number of non-native species currently introduced as pets in the country, and this includes amphibians (Measey et al. 2017); invertebrates (Nelufule et al. 2020; Shivambu et al. 2020b), reptiles (van Wilgen 2010), gastropods (Shivambu et al. 2020a), and rodents (Maligana et al. 2020). Some of these species are prohibited from trade as they pose an invasion risk and are protected under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2021). This suggests that the trade in non-native species as pets should be strictly regulated in the country, and legislation on trade should be implemented and reviewed. The traded species are regulated under the National Environmental Management: Biodiversity Act (NEM:BA) of 2004 (DEA 2016). This legislation prohibits the sale of several species, including some small mammalian species. However, the legislation does not prohibit the sale of some pet species already invasive in the country, for example, the Norwegian rat *Rattus norvegicus* and house mouse *Mus musculus* (Maligana et al. 2020).

1.1.8 Mammal pets in South Africa

In South Africa, mammals have been introduced through various vectors including, hunting, biological control, farming, stowaway, ornamental and pet trade (Measey et al. 2020). However, the pet trade and ornamental trade represent 4% of the invasive species (Measey et al. 2020). Mammalian species introduced for different purposes are now kept as pets in the country; for example, the *O. cuniculus* was introduced as a farm animal, but it is now one of the most popular of small mammal pets (Shivambu et al. 2020d). Currently, only four small mammalian species kept as pets are recorded as invasive species, i.e. *R. norvegicus*, *M.*

musculus, *O. cuniculus* and *S. carolinensis*. The invasion of *R. norvegicus* and *M. musculus* is not associated with the pet trade but with the accidental introduction of stowaways (Measey et al. 2020). However, Maligana et al. (2018) reported rats with the typical markings of pet and laboratory rats with red eyes in Alexandra township, South Africa. These rats have become successful invaders in the township and are associated with economic and health impacts on humans (Maligana et al. 2018). Most mammalian species' success as unwanted feral or biological invaders is associated with traits such as extensive physiological tolerance, neophobic behaviour, high reproduction rates, association with humans, broad habitats and diets (Long 2003; Clout and Russell 2007; Latham et al. 2017).

1.2 Study motivation

The exploitation of wildlife for the non-native pet trade and their potential as invasive species motivated this study in South Africa. The topic is sensitive and has been debated upon as it embraces broad societal issues such as generating employment and contributing to the economy (Kroeger 2007). The global legal and illegal trade on wildlife and its products is estimated at US$300 billion per annum and US$5–20 billion, respectively (Smith et al. 2017). Although there are some advantages of the pet trade, its consequences on biodiversity, economy and society can be dire. Protected species under international laws such as CITES can become vulnerable to extinction because of removal from their native distribution ranges. For example, primates such as marmosets *Callithrix* spp. are listed under CITES; however, several species are illegally traded to different countries (Susanne and Ann-Kathrin 2005; Carvalho et al. 2013). In addition, *O. cuniculus* is listed as endangered and vulnerable to extinction in its native distribution range; however, this species has become invasive in various countries through accidental escape and intentional release of pets and farmed animals (Long 2003; Measey et al. 2020).

Escaped and released small mammal pets such as *P. breviceps*, *M. putorius furo*, *C. jacchus* and *S. carolinensis* have been implicated in causing the decline of native fauna through competition, predation, and disease transmission (Stojanovic et al. 2017; Campbell et al. 2018). These established pets have also impacted human lives by transmitting zoonotic diseases, negatively impacting agriculture and forestry production (Byrom 2002; Halsby et al. 2017; Childs et al. 2019). In addition, once these species become invasive, they are not easy to eradicate, and the cost associated with their eradication plans may be enormous (Pimentel et al. 2000; Williams et al. 2010; Jardine and Sanchirico 2018). For example, the total damage and management costs of *S. carolinensis* in Britain was estimated at £14 million per annum in 2010 (Williams et al. 2010). Small mammals that are already kept in captivity as pets, or that are likely to be imported as pets into South Africa may pose the risk of becoming invasive if released or escape from captivity. Consequently, if these pets are released or escape from captivity, they could threaten South Africa's biodiversity, economy and human health. It is therefore important to assess the pet trade industry in South Africa so that an inventory of species that poses an invasion potential can be compiled. The inventory will also enable proper risk assessments, which can be used when drafting policies and management of traded species. The use of molecular analyses in determining the identity and genetic diversity of some of these species may help evaluate the distribution of the traded species in South Africa. In addition, molecular analyses could help determine the invasion potential of the species with high genetic variation.

1.3 Study aims and objectives

Given the above background, this study aimed to determine the extent of trade in non-native small mammals, potential environmental and socio-economic impacts as well as their potential distribution and genetic diversity. The following main research objectives were established:

1. Survey physical pet shops and online websites in South Africa to get an overview of the extent of trade in non-native small mammals in the country. This includes determining which non-native small mammalian species are sold, commonly available on the trade and their prices. It was predicted that online trade would offer more non-native small mammalian species than pet shops as online trade is poorly regulated, and there is typically lower compliance with existing regulations. It was further predicted that rarer species would be offered at relatively high prices than other species.
2. Conduct survey questionnaires to investigate the species composition across the provinces and determine which small mammalian species are sold by the pet shop owners. Investigate the sources from where pet shops acquire their non-native small mammals; and if the pet shops are aware of the regulations which govern the sale of non-native pets. It was predicted that rodents would be the most popular species traded because they are relatively easy to maintain, are cheaper, and often sold as feeders for reptiles such as snakes. It was also predicted that pet shop owners acquire their pets from different sources, and most of them are aware of the NEM: BA regulation.
3. Review the literature on the impacts associated with non-native small mammals to determine the environmental and socio-economic impacts associated with them. It was predicted that most of the non-native small mammalian species traded as pets in South Africa would be more associated with socio-economic impacts rather than environmental impacts.
4. Use native and introduced occurrence records to evaluate the potential distribution based on ecological niches (species distribution modelling (SDM)) and the human footprint. It was predicted that species with high availability, history of invasion elsewhere and extensive occurrence records would have greater invasion potential. In

addition, we expected the human footprint to influence the potential distribution of *M. musculus* and *R. norvegicus*.

5. Use mitochondrial gene data to identify, evaluate genetic diversity and geographical patterns of some rodent species in the South African pet shops. It was predicted that there is genetic diversity within the rodent species sold in South African pet shops, and their genetic diversity follows a clear geographically correlated pattern.

1.4 Thesis outline

This thesis consists of seven chapters, of which five are data chapters (2 to 6) that can be read independently. Each data chapter is prepared for publication in a relevant peer-reviewed journal, some are already published, and therefore some overlap and repetitions were unavoidable. The chapters are as follows:

1. **Chapter 1:** General introduction
2. **Chapter 2:** Non-native small mammal species in the South African pet trade
3. **Chapter 3:** A survey of non-native small mammals traded in South Africa: Pet shop owners' perceptions
4. **Chapter 4:** Assessing the potential impacts of non-native small mammals in the South African pet trade
5. **Chapter 5:** Predicting the potential distribution of non-native small mammalian species sold in the South African pet trade
6. **Chapter 6:** Genetic diversity of non-native small mammal species sold in the South African pet shops
7. **Chapter 7:** General discussion and conclusions

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CHAPTER 2

Non-native small mammal species in the South African pet trade

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2.1 Abstract

Non-native small mammals are amongst the most popular species traded as pets around the world. Some of these mammals have become invasive through various pet trade releases and escapees in most countries. In South Africa, several non-native small mammals have been introduced for pet trade purposes. We assessed the sale of non-native small mammals in South Africa from September 2018 to 2019 to determine their abundance and degree of trade online and in pet shops. A total of seven websites were recorded selling 2,681 individuals representing 24 species belonging to seven taxonomic orders. For physical pet shops, 19,391 individuals representing 16 species and seven orders were recorded from 122 pet shops. Rodents and primates were the most dominant groups in both online and pet shops. The most common small mammal species traded were the Norwegian rat *Rattus norvegicus*, the guinea pig *Cavia porcellus*, the European rabbit *Oryctolagus cuniculus* and the house mouse *Mus musculus*. Prices ranged from ZAR9.00 to ZAR12,000.00, with rodents offered at relatively low prices. The most abundant species traded were relatively cheap when compared with the least abundant species, and CITES species were more expensive than non-CITES species. Species with high abundances traded at low prices and have a history of invasion through pet trade releases and escapes pose an invasion risk in South Africa. Therefore, their trade should be strictly regulated.

Key words: biological invasion, introduction pathways, pet shops, policy, online trade

2.2 Introduction

Non-native species have been deliberately and accidentally introduced around the world through different pathways (Hulme 2009; Mori et al. 2017; Lockwood et al. 2019). Examples of accidental introductions include hitch-hikers or contaminants of transported goods, while hunting, biocontrol, fishing and pet trade are considered as deliberate introductions (Keller et al. 2011; Britton and Orsi 2012; Faulkner et al. 2016; Ng et al. 2016; Carpio et al. 2020). The trade of non-native pets is one of the growing consumer trends for many societies around the world (Micheli 2014; Lockwood et al. 2019; Carpio et al. 2020; Shivambu et al. 2020a, b). The pet trade industry makes millions of dollars for business owners, and it has been reported that the international legal trade in live non-native animals is worth ~ US$451.48 million (Durand et al. 2013; Robinson et al. 2015). For example, the reptile pet trade industry in the UK is estimated to be worth ~ US$260.6 million, with a reported ~ 250,000 amphibians and reptiles bred for the pet trade industry every year (Herrel and van der Meijden 2014; Robinson et al. 2015). Small mammals, especially rodents, are increasingly becoming the most popular pets in the world (Ellis and Mori 2001; Grant et al. 2017). The American Veterinary Medical Association (AVMA) indicated that between 2007 and 2012, the number of households that keep rodents in the USA had increased by 11% (Lankau et al. 2017). An online search in the USA by Lankau et al. (2017) showed that rodents such as chinchillas (e.g. *Chinchilla chinchilla*, *C. lanigera*), hamsters (e.g. *Mesocricetus auratus*, *Crecetus grideus*, *Phodopus campbelli*, *P. roborovskii*), gerbils *Meriones unguiculatus*, guinea pigs *Cavia porcellus*, mice (e.g. *Mus musculus*, *M. musculus domesticus*), and rats (e.g. *Rattus norvegicus*) are sold on the internet and are listed on pet shop websites.

Online trade has been shown as an important pathway for non-native species invasions as traders can move different non-native pets relatively easily from one place to another (Kikillus et al. 2012; Mazza et al. 2015; Canlas et al. 2017; Shivambu et al. 2020c). Although trade bans can reduce movement and the risk of invasion (Cardador et al. 2017, 2019), studies have indicated that prohibited non-native pets continue to be sold via online portals, e.g. Faulkes (2018) indicated that prohibited crayfish species are sold online, and Siriwat and Nijman (2018) showed that prohibited otter species listed on the Convention on International Trade in Endangered Species (CITES) are largely sold online. In addition, the online trade offers almost any type of non-native pet species as opposed to the physical pet shops, which are generally easier to regulate and are subject to inspection (Marano et al. 2007; Pasmans et al. 2017; Shivambu et al. 2020b). Increased usage and ease of access to the internet has contributed to the introductory pathways of invasions; however, the internet, as an invasion pathway, has mostly been overlooked by policy-makers and researchers (Derraik and Phillips 2010; Martin and Coetzee 2011; Lenda et al. 2014; Mazza et al. 2015). Consequently, the sale of species through the internet may likely increase in the future as it has been indicated to increase the accessibility of a wide range of taxa (Gastañaga et al. 2010; Bush et al. 2014; Daut et al. 2015).

Most households with non-native pets obtain these from either breeders, rescue clubs, pet shops, and/or through online trade (Meenken 2012; Halsby et al. 2014; Stoakes 2014; Neville et al. 2019). Non-native small mammal species are also commonly traded via online portals and pet shops as feed for other non-native pets such as snakes, e.g. ball python *Python regius* and the red-tailed boa *Boa constrictor* (Cooper and Williams 2014; Kanagarajah et al. 2018). An increase in the trade of these non-native small mammal species as pets is of great concern for human and predator pets' health as most of these species are associated with zoonotic agents such as *Salmonella*, *Francisella tularensis*, monkeypox virus and *Yersinia pestis* (Inoue et al. 2009; Lankau et al. 2017; Kanagarajah et al. 2018). Some of the non-native small mammal species traded as pets pose a risk of becoming invasive if released or escape from captivity, e.g. the black-tailed prairie dog *Cynomys ludovicianus* in North Central Florida

(Hardin et al. 2014) and Siberian chipmunks *Tamias sibiricus barberi* in Europe (Marsot et al. 2013; Mori et al. 2018).

In Brazil, da Rosa et al. (2017) indicated that 70% of identified non-native mammal species became invasive because of deliberate release or escape from breeding facilities. Most of the escaped or released pet mammal species are associated with negative impacts (Shivambu et al. 2020c); for example, the sugar glider *Petaurus breviceps* in Tasmania has been reported to negatively impact biodiversity by preying on tree cavity-nesting birds (Stojanovic et al. 2017; Campbell et al. 2018). It has been reported that most of the non-native species which become invasive are those that have relatively high availability, easy to breed in captivity and sold at generally low prices in the pet trade (van Wilgen et al. 2010; Stringham and Lockwood 2018; Lockwood et al. 2019). Non-native small mammal species are generally considered easy to care for, relatively cheap to maintain and are inexpensive pets to purchase (Quesenberry and Carpenter 2011; Sirois 2016).

In South Africa, non-native small mammal species such as the Norwegian rat and house mouse are sold as companion pets (Maligana et al. 2020). However, the role of the pet trade as an introduction pathway for most non-native small mammals has not been thoroughly evaluated across South Africa, and few species are regulated under the National Environmental Management: Biodiversity Act (NEM:BA) (DEA 2016). Species such as the Norwegian rat, house mouse and European rabbit *Oryctolagus cuniculus* are listed under NEM:BA as category 1b for off-shore islands. According to this regulation, these three species may not be owned, imported into South Africa, moved, sold and given as a gift only in the South African off-shore islands. There is currently no regulation that prevents the selling, importing or breeding of these three species in mainland South Africa. Additionally, the eastern grey squirrel *Sciurus carolinensis* is listed under category 1a in KwaZulu-Natal Province and category 3 in other provinces (DEA 2016). Category 1a prohibits a species from being imported, possessed, bred, moved, sold, and accepted as a gift, while category 3 does not prohibit and requires a permit for trade. Although listed, these four species are established in South Africa and its off-shore islands (Picker and Griffiths 2017; Measey et al. 2020). Additionally, little is currently known about which non-native small mammal species are sold nor their trade volume. There is also a paucity of information on how trade in non-native small mammal species sold in South Africa varies between online portals and physical pet shops. In our present study, we, therefore, aimed to 1) determine which non-native small mammal species were sold in South Africa, including their relative abundance and richness in the online and pet shop trade; 2) determine invasion history and introduction pathways for these small mammal species; 3) determine their prices in the two trade platforms; and 4) investigate if the price is determined by species availability, IUCN (International Union for Conservation of Nature) conservation, CITES status, and invasion status. We predicted that online trade would offer more non-native small mammal species than pet shops as online trade is poorly regulated and there is typically lower compliance with existing regulations, and so any type of non-native pet can be easily sold (Marano et al. 2007; Pasmans et al. 2017). We further predicted that rarer species would be offered at relatively high prices than other species. For example, CITES-listed species were predicted to be more expensive compared with other species, and least concern species were predicted to be cheaper compared with other species.

2.3 Materials and methods

2.3.1 Pet shops

We located the geographical locations of physical pet shops that sold non-native small mammal species in the provinces of South Africa (Fig. 2.1), by identifying them through Google maps and Google earth. We also searched the South African pet shop directory (http://www.pet-shops.co.za/Manual/ locate-petshop-in-south-africa.html) and the South African Pet Traders

Association website (http://www.sapettraders.co.za/membership-2016/) for any listed physical pet shops. We collated a database of all physical pet shops present in South Africa and created a heat map to indicate their distribution using ArcGIS version 10.4 (Environmental Systems Research Institute 2018, Fig. 2.1). We found most of these pet shops located within shopping centres in the city centres and towns near major cities (Fig. 2.1).

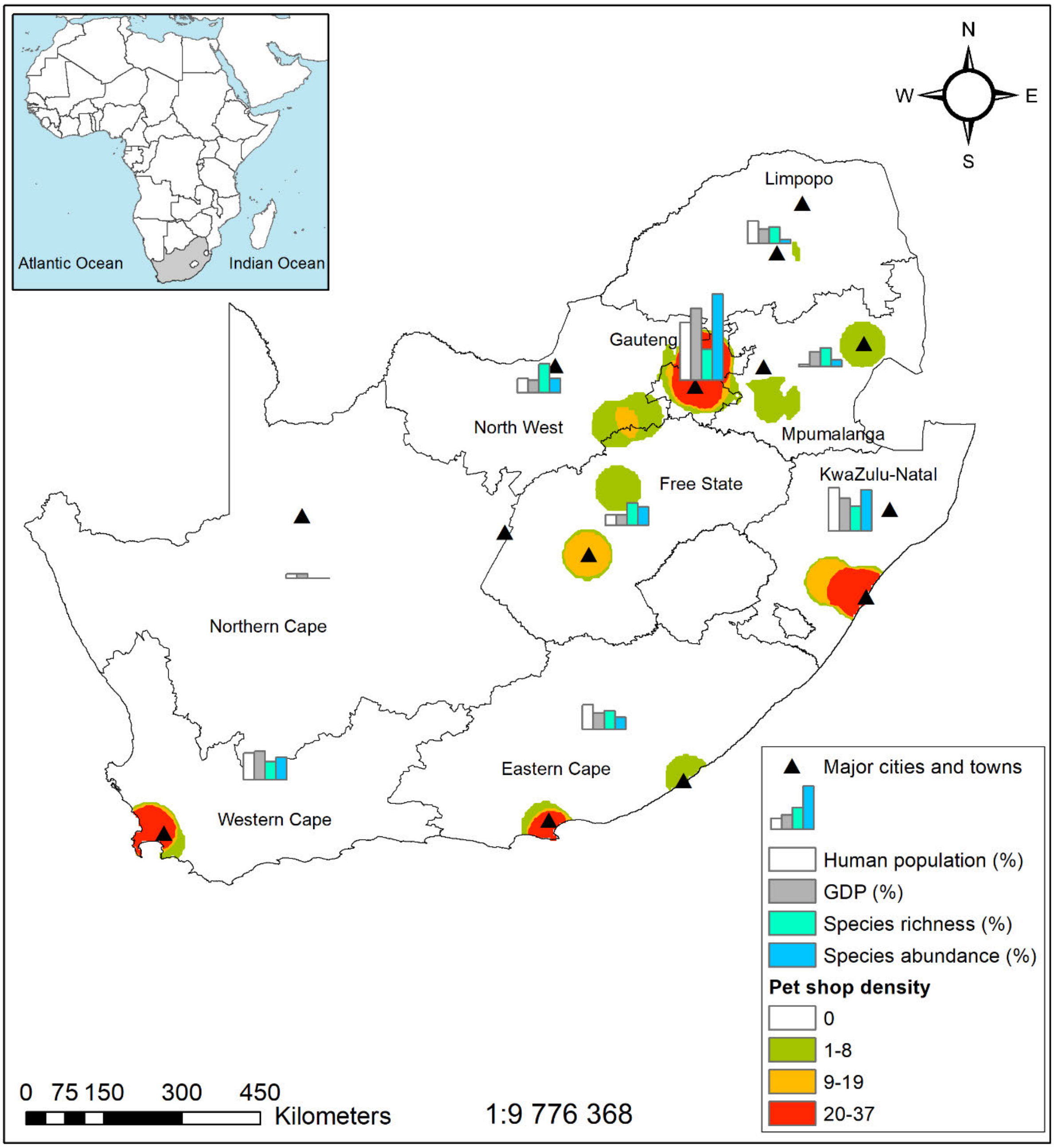

Fig. 2.1 Heatmap summarising the distribution of physical pet shops surveyed between September 2018 to September 2019 in South Africa. The bar chart indicates the relative percentage of the total human population and gross domestic product (GDP) of the country, species richness and abundance for non-native small mammals available for sale in the pet trade.

Each pet shop was visited once in September 2018, December 2018, April 2019, and June 2019 to find if there were any new species advertised that we could not have recorded in the previous sampling. This was done because pet shops are likely to import different animals in different seasons from various countries, as reported in Shiau et al. (2006) and Faulkes (2015). Pet shops that were not open in September 2018 were surveyed in September 2019. In total, each pet shop was visited four times. We excluded all the pet shops which only sold pet products from our pet shop list and surveyed those pet shops which sold live non-native animals. We conducted general observations in each pet shop to record the following in a database: 1) date of visit; 2) province where pet shop was situated; 3) common and scientific names of each of the small mammal species available for sale; 4) number and age class (juvenile, adult) of individuals of each recorded species; and 5) displayed price for each recorded small mammal species. An opportunistic survey was conducted to get information about the species of small mammals traded. The owners or workers were asked general questions, including how often they receive new livestock from their suppliers and how long individual species last in the store before they are purchased. This was done to minimise duplication of the pet shop dataset. Additionally, if the same individual species was still not purchased on our follow up visit, we did not record that species. This was often the case for rare species such as ferrets *Mustela putorious furo*, sugar gliders and primates. Most of the small mammal species were displayed with their common names only, but in some of the pet shops, scientific names were also provided (Supplementary material Fig. S2.1). Some of the pet shop owners were experienced breeders and some zoologists; this made the process to identify the species easier. We obtained human ethic approval to conduct the surveys by the University of KwaZulu-Natal, Humanities and Social Research Ethics Committee (Permit number: HSS/0908/018D).

2.3.2 Online small mammal species trade

We conducted an online assessment of small mammal species between September 2018 and September 2019. We collated information on the small mammal pet species listed for sale on Facebook and South African advertising websites (Supplementary material Fig. S2.2). Search terms such as "small mammals for sale", "mammals for sale" and "non-native pets" were used. We further expanded the searches by using the common name of each species, e.g. "rats, mice, ferret, chinchilla, fennec fox, kinkajou, tenrec, rabbit, guinea pig, degu, sugar glider, and hamster or monkey for sale". We checked the sales four times each month within a year to establish if there were any new listings on the adverting websites and Facebook. We also recorded the following for any small mammal species sold online: 1) the date of the advertisement; 2) the province where the species was sold from; 3) the name of the small mammal species traded; 4) the number and age class (juvenile, adult) of individuals of each species available for sale; and 5) the price of each recorded individual. All the non-native small mammal species available for sale in the online trade were mainly sold under their common names and not scientific names (Supplementary material Fig. S2.2). We, therefore, identified all the taxa to species level using personal experience and, where necessary, identification guides were used (Turner 2004; Petter and Desbordes 2013; Couzens et al. 2017; Kingdon 2019). To minimise duplication for the online dataset, we compared the photographs posted by different advertisers and in different regions of advertisement, as advertisers can post the same individuals using different advertising websites. Again, some advertising websites allow for the advertisement to be active for two months, so we were able to notice if the advertisement was repeated or new. Advertisements without pictures were excluded in this study as it was not possible to identify the species. For Facebook, we differentiated the advertisements by checking different users and different animal images posted. Again, on Facebook sites, only

5,000 pictures can be displayed at a time, and older ones are automatically removed when new images are received (Iqbal 2016).

2.3.3 Data analyses

All data were analysed using R statistical software (version 3.4.4, R Core Team 2018). We averaged the number of species sold for both online and pet shop trade respectively to determine the most abundant species, the species richness and abundance per province. We used the Mann-Whitney U test to compare the species abundance based on pairs of replicates in online trade and pet shops. The Kolmogorov-Smirnov normality test was used to determine if data were normally distributed, independent, and identical. As a result, we found that the data were not normally distributed. We, therefore, used a Kruskal-Wallis test by ranks to determine which species was abundant and used a Mann-Whitney pairwise test with Bonferroni p values adjusted at 0.01 to determine the differences between the groups. We examined the relationship between the number of individuals of each species and their overall price using linear regression with the Pearson correlation test. The data for linear regression was log-transformed to reduce the highly skewed distributed data to normal. Linear regression models were used to determine the relationship between each variable (species number, CITES-listed, IUCN status, non-invasive and invasive in South Africa and elsewhere) and price. The Akaike Information Criterion (AIC) was used to identify the model with the greatest explanatory power. We used the Kruskal-Wallis test by ranks and the Mann-Whitney pairwise tests to determine the price differences between CITES and Non-CITES listed species, between the different IUCN statuses and invasion status.

2.4 Results

We found a total of 122 physical pet shops selling 19,391 individuals representing 16 non-native small mammal species and seven online advertising websites selling 2,681 individuals representing 24 species (Supplementary material Table S2.1). Only one native species, the southern multimammate mouse *Mastomys coucha* was recorded, but this rodent was excluded from further analyses. We found out that there were no additional new species in the pet shops during follow-up visits. However, for online sampling, a total of 10 new species were recorded during the follow-up searches (Supplementary material Table S2.2). The recorded species belonged to seven orders, with Rodentia being the most dominant order representing more than 40% of all species for sale (ten species) in both online platforms and pet shops (Supplementary material Table S2.2). The second largest group was the primates, which represented 29% (seven species) of species for sale in the online trade and 12% (two species) of the species for sale in the pet shop trade. Carnivores contributed 13% (three species) of the online trade compared with 6% (one species) of the pet shop trade (Supplementary material Table S2.2). The other remaining groups, including the Eulipotyphla, Afrosoricida, Lagomorpha and Diprotodontia, together contributed 4% of online trade and 6% of the pet shop trade (Supplementary material Table S2.2). Most of the online advertisements were recorded from Gauteng Province (number of adverting websites (n) = 7), KwaZulu-Natal Province (n = 7), and Western Cape Province (n = 6), followed by the Eastern Cape Province (n = 4), and Mpumalanga Province (n = 4) (Supplementary material Table S2.1). The Free State Province (n = 3), North West Province (n = 3), Northern Cape Province (n = 3), and Limpopo Province (n = 2) had the least number of websites advertising non-native small mammal species per province (Supplementary material Table S2.1).

The provinces with the highest numbers of pet shops were Gauteng Province (number of pet shops (n) = 37), KwaZulu-Natal Province (n = 27), and the Western Cape Province (n = 20) (Supplementary material Table S2.1). Some provinces, such as Limpopo (n = 3) and Northern Cape Province (n = 2), had only a few pet shops selling non-native small mammal species (Table S2.1, Fig. 2.1). In terms of online trade per province, Gauteng Province recorded a total of 1,160 individuals representing 24 species (Supplementary material Table S2.1). This was followed by KwaZulu-Natal Province, which recorded 800 individuals (n = 15 species) and the Western Cape Province, which recorded 421 individuals (n = 11 species) (Table S2.1). Other provinces recorded less than 200 individuals for sale, with the Eastern Cape and Mpumalanga Provinces representing 11 species each and other provinces representing less than six species (Supplementary material Table S2.1).

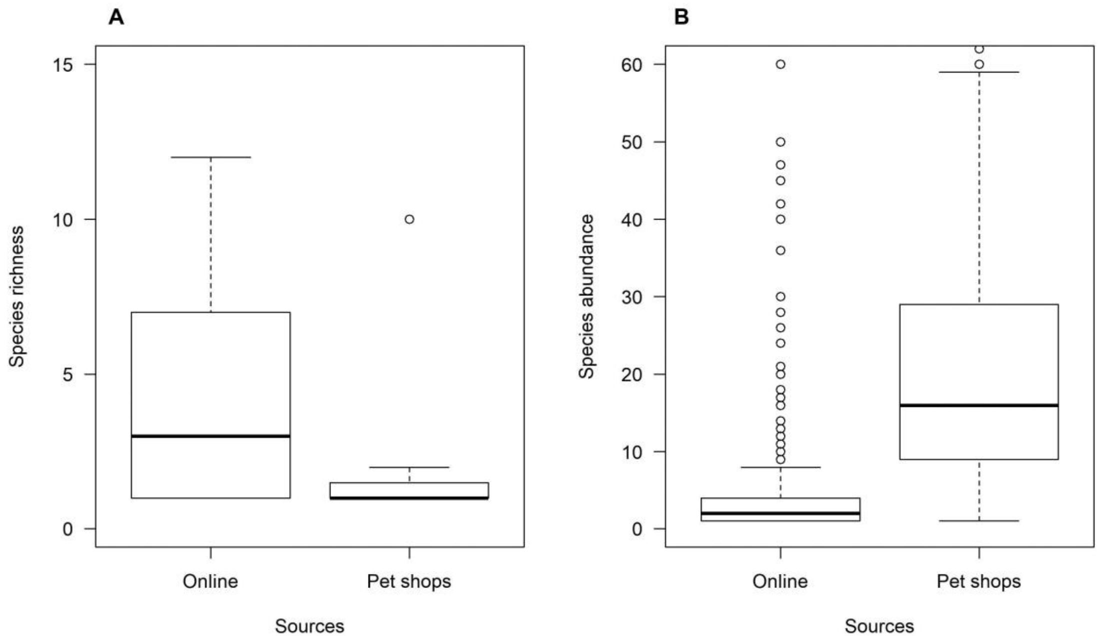

Fig. 2.2 Non-native small mammal species sold in South Africa from September 2018 to September 2019 where (A) shows the mean number of species available in the online trade (max = 24 species) and pet shops (max = 16), and (B) shows their mean abundance in online trade (total abundance = 2,681) and pet shop (total abundance = 19,391).

In terms of numbers in physical pet shops per province, Gauteng Province recorded the highest number of individuals, i.e. 8,199 representing 15 species. This was followed by KwaZulu-Natal Province, which recorded 3,946 individuals (n = 12 species), the Western Cape Province with 2,191 individuals (n = 9), and North West Province with 1,393 individuals (n = 14) (Supplementary material Table S2.1). Free State, Eastern Cape, Mpumalanga, and Limpopo Provinces recorded less than ten small mammal species represented by 1,644, 1,043, 578 and 387 individuals, respectively (Supplementary material Table S2.1). We did not record any small mammal species for sale in the Northern Cape Province physical pet shops (Supplementary material Table S2.1). In terms of species richness in the online and pet shop trade, we found no significant difference between the number of species traded online compared with pet shops (Mann-Whitney U test, U = 20; P = 0.56; Fig. 2.2a). The overall species abundance available for online trade was significantly lower than the overall species abundance in the pet shops (Mann-Whitney U test, U = 39869, P = 2,46e−165; Fig. 2.2b).

We found a significant difference in the number of each of the small mammal species available for sale online (Kruskal-Wallis χ^2 = 59.46; df = 23; P = 6,28e−05; Fig. 2.3a). The mean number of European rabbits for sale online was significantly higher than the mean number for the other 23 species (Fig. 2.3a). Species such as the Norwegian rat, the house mouse, the guinea pig, the dwarf hamster *Phodopus sungros,* and the sugar glider also had a significantly higher mean number available for sale than the other species (Fig. 2.3a). The least available species were the common squirrel monkey *Saimiri sciurus*, eastern grey squirrel, and cotton-top tamarin *Saguinus oedipus* (Fig. 2.3a).

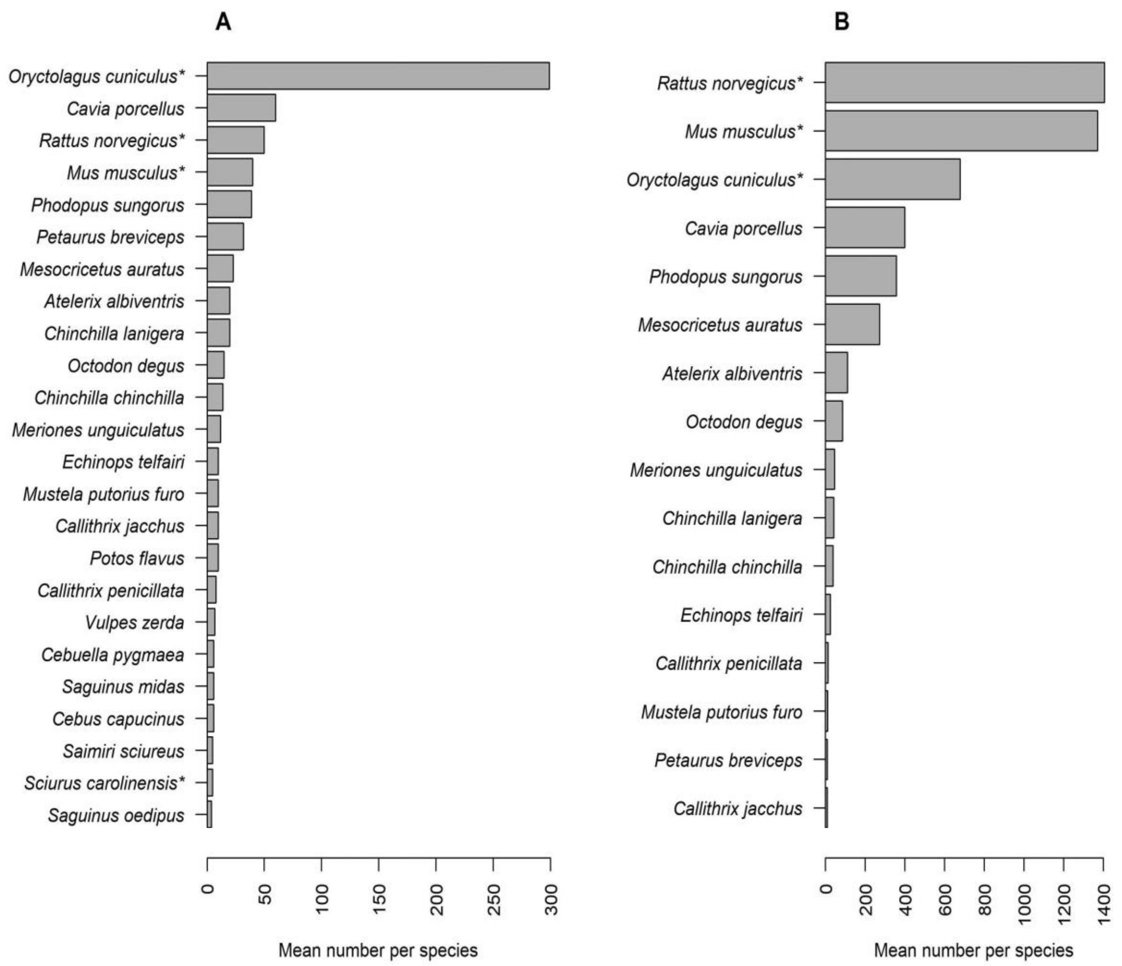

Fig. 2.3 The mean number of the recorded small mammal species advertised for sale in South African a) online trade and b) pet shops between September 2018 and September 2019. An asterisk (*) indicates established non-native species in South Africa.

There was a significant difference in the number of individuals of each non-native small mammal species sold in the physical pet shops (Kruskal-Wallis $\chi^2 = 62.67$; df = 16; $P = 0.0084$; Fig. 2.3b). The most abundant species for sale in terms of mean number included the Norwegian rat, the house mouse and the European rabbit (Fig. 2.3b). Guinea pigs, dwarf hamsters, and golden hamsters were also common species in terms of numbers in the pet shops (Fig. 2.3b). The least common species in the pet shops included the black tufted-ear marmoset, the ferret, the sugar glider, and the common marmoset (Fig. 2.3b). Eight species that were recorded in the online trade but not in the pet shops included the pygmy marmoset *Cebuella* *pygmaea*, the red-handed tamarin *Saguinus midas*, the cotton-top tamarin, the common squirrel monkey, the eastern grey squirrel, the white-faced capuchin *Cebus capucinus*, the fennec fox *Vulpes zerda*, and the kinkajou *Potos flavus* (Fig. 2.3b). The conservation status of about 67% (number of species (n) = 16) of small mammals traded was the least concern, 13% (n = 3) of the species are listed as endangered, and 8% (n = 2) are listed as vulnerable to extinction and not evaluated. Only one species (4%) was listed as critically endangered (Table S2.2). Furthermore, we found that 54% (n = 13) of small mammal species were not listed on CITES, and this included mostly rodent species (39%; n = 10). In contrast, most primate species were listed on CITES (Table S2.2). Nine species have established feral populations in most countries (Table S2.3). Of these, only four, including the Norwegian rat, house mouse, European rabbit and eastern grey squirrel, were recorded as established in South Africa (Fig. 2.3a, b; Supplementary material Table S2.3). The introduction pathway for these species included pet trade, ornamentation, farming, hunting and stowaways (Supplementary material Table S2.3).

The mean price per small mammal species available for sale in the present study ranged from ZAR9.00 to ZAR12,000.00 (Supplementary material Table S2.2). The least expensive species for both the online trade and pet shops were rodent species which ranged between ZAR9.00 and ZAR250.00 (Supplementary material Table S2.2). These included species such as house mice, Norwegian rats, dwarf hamsters, golden hamsters, common degus *Octodon degus*, Mongolian gerbils *Meriones unguiculatus*, and guinea pigs (Table S2.2). Species that cost more than ZAR1,000.00 included domesticated ferrets, sugar gliders, chinchillas, kinkajous and eastern grey squirrels (Supplementary material Table S2.2). The most expensive species recorded were the primates, as they cost more than ZAR3,000.00 each (Supplementary material Table S2.2). Nonetheless, red-handed tamarin was the most expensive of all species, and it is listed as critically endangered under CITES Appendix I (Supplementary material Table S2.2). For species such as chinchillas, domesticated ferrets and lesser hedgehog tenrecs, the mean online prices were lower than the pet shops prices (Supplementary material Table S2.2). Overall, least concern species such as the Norwegian rat and house mouse were sold at relatively low prices compared with the other small mammal species (Supplementary material Table S2.2). There were no significant differences in the mean price of non-native small mammal species sold online compared with pet shops (Mann-Whitney U test, U = 108; P = 0.22). Small mammal species abundance and retail prices for both online ($r^2 = -0.58$; P = 2.2e−16) and physical pet shops ($r^2 = -0.12$; P = 2.2e−16; Fig. 2.4) showed a negative linear relationship, with the least abundant species (number of individuals available for sale) sold at relatively high prices compared with abundant species (Fig. 2.4).

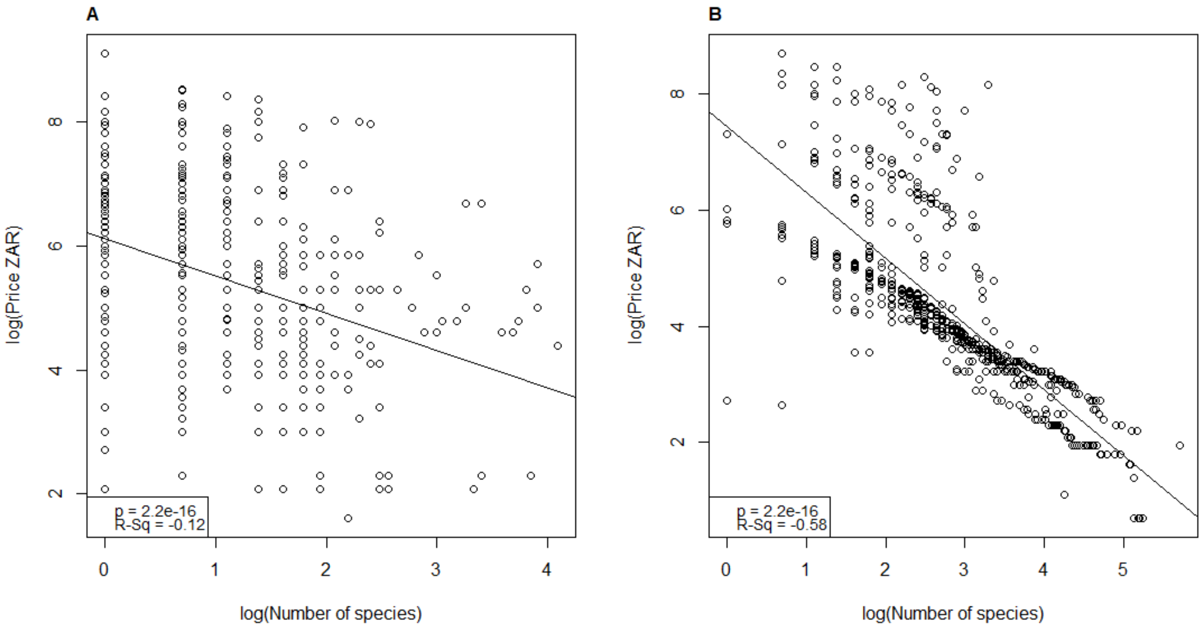

Fig. 2.4 The relationship between log price and log number of non-native small mammal species recorded in the current study in a) pet shops and b) online trade in South Africa.

When comparing the mean prices of small mammal pets according to their conservation status, there was a significant difference between the means for online sales (Kruskal-Wallis χ^2 = 45.70; df = 4; P = 2.73e−09; Fig. S2.3a). Furthermore, critically endangered species were offered at relatively higher prices when compared with the other species status categories (Mann-Whitney pairwise test; $P < 0.001$, Bonferroni corrected p values; Supplementary material Fig. S2.3a). For pet shops, there was a significant difference on the mean prices of the small mammal species on sale between conservation status (Kruskal-Wallis $\chi^2 = 82.25$; df = 3; $P = 1e{-17}$; Supplementary material Fig. S2.3b). Again, CITES-listed species were offered at higher prices when compared with non-CITES species (Supplementary material Fig. S2.1c, d). The mean price of species listed on CITES under Appendix I, II, III and non-CITES were significantly different for online sales (Kruskal-Wallis $\chi^2 = 173.2$; df = 3; $P = 2.78e{-37}$; Supplementary material Fig. S2.3c). Appendix II and III species were offered at higher prices than Appendix I and non-CITES species (Supplementary material Fig. S2.3c). For prices in pet shops, the mean price of species listed on CITES under Appendix I, II, and non-CITES were significantly different (Kruskal-Wallis $\chi^2 = 97.3$; df = 2; $P = 7.30e{-22}$; Supplementary material Fig. S2.3d). Appendix II species were offered at higher prices compared with Appendix I and non-CITES species (Supplementary material Fig. S2.1d). However, when comparing the mean price of Appendix I and non-CITES species, it was found that CITES Appendix I species were offered at higher prices than non-CITES species (Supplementary material Fig. S2.3d). In terms of invasion status, mean prices for species known to be invasive elsewhere were sold at significantly higher prices than non-invasive and invasive species in South Africa for both online (Kruskal-Wallis $\chi^2 = 218$; df = 2; $P = 3.676e{-48}$) and pet shops (Kruskal-Wallis $\chi^2 = 113.5$; df = 2; $P = 2.253e{-25}$) (Supplementary material Fig. S2.3e, f). For online trade, the model showed that price was determined by CITES-listed species (Appendix I), non-CITES, IUCN-listed species (Vulnerable, Least Concern and Endangered), and by all categories for invasion status (invasive elsewhere, invasive in South Africa, and non-invasive) (Supplementary material Table S2.4). Species listed in CITES Appendix I, non-CITES, IUCN least concern and endangered determined the price for pet shop. Price was also determined by all invasion categories for species sold in the pet shops (Supplementary material Table S2.4).

2.5 Discussion

We found that three South African provinces, namely Gauteng, KwaZulu-Natal, and the Western Cape, had the highest number of pet shops and online websites selling non-native small mammal species. These three provinces represent South Africa's most fast-growing economies, and their cities are more populated than other provinces (STATS SA 2019). It has been indicated that an increase in non-native pets is linked to human population growth and economic status (Shepherd et al. 2007; Smith et al. 2017). Furthermore, the pet trade is likely to play a role in the economies of these provinces. However, it has been indicated that a growing human population lead to increased demand for non-native pets (Bush et al. 2014; Lockwood et al. 2019). Consequently, this may pose an invasion risk, particularly for species with very high demand and popularity, e.g. the Norwegian rat, house mouse, European rabbit, and guinea pig. In Japan, the common raccoon *Procyon lotor* became a popular pet, and as a result, it has established feral populations because of accidental escapes and intentional releases (Macdonald et al. 2017). In addition, Gauteng, KwaZulu-Natal, and Western Cape Provinces are at higher risk of becoming invaded given that most of the pet shops are situated in urban areas with high human density (see Banha et al. 2017 and Filz et al. 2018). Although KwaZulu-Natal and Western Cape Provinces had the most pet shops and recorded more individuals, the number of species offered for sale was lower than that in the North West Province, although the latter had relatively few pet shops. This suggests that the number of pet shops is not directly related to species richness. In terms of invasion risk, all the provinces are likely to be invaded despite the fact that their species abundance as invasions are also linked to the type of a species, its reproductive success, lack of predators, broad diet, and ability to tolerate wide climate ranges (Lockwood et al. 2019; Maceda-Veiga et al. 2019; Moraes et al. 2019)

In some of the provinces, we found that more non-native small mammal species were recorded in online trade than in the pet shops, which indicated that most of the sellers in these provinces were private. Online trade offered higher species richness but lower abundance than the pet shops, even though statistical analysis indicated no significant differences in species richness and abundance between the two trade sources. This difference could be explained by that new species were recorded during the follow-up searches in online trade, while no additional species were found during the pet shop revisit. The relatively low species richness in the pet shops could also be explained by increased use of the internet (Gastañaga et al. 2010). In addition, the online trade is generally fast, species can be delivered directly to homes, easily accessed by more people than pet shops, and it is difficult to regulate, making it easy for the traders to sell illegal pets (Marano et al. 2007; Alacs and Georges 2008; Musing et al. 2015; Pasmans et al. 2017). Previous studies indicated that species sold in large volumes are most likely to be intentionally released into the wild as opposed to those traded at low volume (Holmberg et al. 2015; Stringham and Lockwood 2018). In the present study, the most abundant species in the pet shops and online trade were European rabbits, Norwegian rats, house mice, hamsters, and guinea pigs. This showed that these mammal species are traded in relatively large quantities in South Africa and are more likely to increase in their numbers which may lead to intentional release or escape. A study in the Netherlands also found that more rodents were traded online than other mammals (Westbroek 2014). Almost all the pet shops were selling these species in South Africa, and this may explain their abundance. Most rodents, such as the Norwegian rat and house mouse, breed throughout the year and often give birth to more than five litters (Gomez et al. 2008; Modlinska and Pisula 2020). This made them abundant throughout the study period, and as a result, the high reproductive rate leads to the successful establishment of species in the wild (Teixeira et al. 2015; Moraes et al. 2019). We found that the sugar glider was abundant in online trade but not common in pet shops. This suggests that sugar gliders in South Africa are mostly sold by private sellers or breeders rather than pet shops. This species may pose an invasion risk in South Africa, given that they quickly escape enclosures and became invasive in Tasmania, Australia, through accidental escapes (Heinsohn 2004).

In our study, we found a negative relationship between price and species abundance; however, the regression coefficient (r^2) was low in pet shops but not for the online trade. This relationship is also more likely to be determined by other factors such as breed type, coat colour, and life span. Therefore, this warrants further investigation, as documented in Su et al. (2015). In addition, our results were similar to the results of other studies where it was found that price was the most important factor that determines species availability in the pet trade, e.g. in Taiwan (Su et al. 2015), Australia (Vall-llosera and Cassey 2017) and Thailand (Siriwat and Nijman 2018; Siriwat et al. 2019). All these studies showed that the most abundant pet species were cheaper, traded in higher volumes and always available for purchase. Previous studies indicated that species traded in large volumes and cheaper are more likely to be released into the wild (Stringham and Lockwood 2018). Species such as the Norwegian rat, house mouse, European rabbit, and guinea pig are likely to be released, establish and cause impacts as they were traded at a low price and as the price was found to be an important predictor for species with invasive history elsewhere, established in South Africa and non-invasive. The first three species and the eastern grey squirrel are regarded as invasives in South Africa, its off-shore islands and elsewhere (Table S2.3). These species are expected to cause severe impacts, particularly socio-economic (i.e. agricultural production and human infrastructure) (Hagen and Kumschick 2018; Shivambu et al. 2020c; Zengeya et al. 2020). Species traded at low volume and higher prices may also establish feral populations and cause impacts. For example, the eastern grey squirrel which was sold at a higher price, is regarded as an established species through pet release and escapes in South Africa and other countries (Long 2003; Huynh et al. 2010; Measey et al. 2020). In addition, species such as the domesticated ferret, common marmoset, black tufted-ear marmoset, common squirrel monkey, and sugar glider may pose an invasion risk despise their trade volume and price given that they have established feral populations through pet trade releases and escapes in other countries (Svihla 1936; Long 2003; Heinsohn 2004; Rylands and Mendes 2008; Rylands et al. 2008; Camarotti et al. 2015; da Rosa et al. 2017; Table S2.3). Some of these expensive species may show aggressive behaviour leading to intentional release, e.g. domesticated ferrets and primates may attack owners (Hitchcock 1994; Favoretto et al. 2001; Soulsbury et al. 2009).

Some of the CITES-listed and protected IUCN species were expensive and not as abundant in our study. Su et al. (2015) and Siriwat et al. (2019) also found that species listed on CITES and those that are protected were expensive when compared with non-CITES and unprotected species. Most of the CITES-listed and protected species are primates (e.g. pygmy marmoset), and these were the second most traded group in the present study. This group has been reported to be the second most introduced species, mainly for the pet trade and research experiments (Bush et al. 2014; Carpio et al. 2020). Still, there is no legislation preventing them from being traded in South Africa, and news reports indicated that this country imports and also exports these primates, especially to Asia (Macleod 2012). Species such as the European rabbit and golden hamster are non-CITES but listed as endangered and vulnerable to extinction. These species are also cheap and traded in large volumes; as a result, they may be overexploited in their native ranges and may pose an invasion risk in areas where they are traded; this is the case for the European rabbit.

2.6 Recommendations and conclusions

Based on the results obtained from the present study, we recommend that the non-native pet trade in South Africa is regularly monitored. Priority should be given to species with high availability, sold at low prices, and known to be invasive through pet release and escapes, e.g. the European rabbit, house mouse, Norwegian rat, eastern grey squirrel, sugar glider, and ferret. These species have also been found to pose either potential high environmental and socio-economic impacts (Shivambu et al. 2020c). We, therefore, recommend that detailed risk analysis (see Kumschick et al. 2020) and species distribution modelling for all non-native mammal species traded be conducted as part of rapid screening. Species currently not included in the national list of non-native and invasive species (i.e. National Environmental Management: Biodiversity Act, 2004 (NEM: BA)) as described in Moshobane et al. (2019) should be included.

Pet shop owners should be advised to provide flyers that explain the importance of not giving away the species or releasing them into the wild, as many of these species have been reported to have established in the wild in other countries through the pet trade (da Rosa et al. 2017; Stojanovic et al. 2017; Campbell et al. 2018). Individual hobbyists who keep or breed any of these pets must be encouraged to apply for a permit (as described in DEA 2014), and if they are buying a potential problematic species, such as the sugar glider or ferret, the males should be castrated. South Africa should have one regulation that applies to all the provinces. Each province currently has its own legislation, and people can buy species prohibited in their provinces from other provinces where the desired species are not prohibited. Pet shop owners should be prohibited from breeding more animals because this may increase the population of the species leading to unintentional escapes and intentional releases if the species are not selling well. The online trade is highly unregulated, especially social media, where any non-native species are sold despite their prohibited status. The trade of the non-native small mammal species is relatively large in South Africa as different species are sold in different provinces. Given this, we recommend stricter law enforcement on online sales. Species sold at low prices, non-CITES, listed as vulnerable or endangered, and that pose a risk of becoming invasive should be protected from trade to prevent extinction and invasion risk.

2.7 Acknowledgements

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2.9 Supplementary material

Supplementary material Table S2.1 The total number of online websites, number of non-native small mammal species recorded, and the total abundance of species available online and in pet shops recorded per province in South Africa between September 2018 and 2019.

Province	Online			Pet shops		
	Number of online advertisements	**Species number**	**Total abundance recorded**	**Number of pet shops**	**Species number**	**Total abundance recorded**
Gauteng	7	24	1,16	37	15	8,191
North West	4	5	40	8	14	1,393
KwaZulu-Natal	7	15	800	27	12	3,946
Free State	6	4	35	10	11	1,654
Western Cape	4	11	421	20	9	2,191
Mpumalanga	3	11	60	6	9	578
Eastern Cape	3	11	112	9	9	1,043
Limpopo	3	3	33	3	8	387
Northern Cape	2	3	20	0	0	0
Sum	N/A	N/A	2,681	122	N/A	19,391

Supplementary material Table S2.2 Small mammal species advertised for sale in pet shops and online platforms in South Africa between September 2018 and September 2019.

Scientific name	Common name	Order	IUCN	CITES status	Native origin	Pet shop				Online			
						No. of pet shops	No. of SA provinces	Total no. of individuals advertised	Mean price (ZAR)	No. of websites	No. of SA provinces	Total no. of individuals advertised	Mean price (ZAR)
Atelerix albiventris (Wagner, 1841)	Four-toed hedgehog	Erinaceomorpha	LC	Non-CITES	Eastern Africa	29	6	812	2,633	6	6	81	820
Callithrix jacchus (Linnaeus, 1758)	Common marmoset	Primate	LC	Appendix II	East-central Brazil	2	2	121	5,7	4	3	40	5,256
Callithrix penicillata (É.Geoffroy Saint-Hilaire, 1812)	Black tufted-ear marmoset	Primate	LC	Appendix II	East-central Brazil	3	1	119	6,375	2	1	37	6,317
Cavia porcellus (Linnaeus, 1758)	Guinea pig	Rodentia	NE	Non-CITES	South America	70	8	3,192	832	3	8	270	266
Cebuella pygmaea (Spix, 1823) ∆	Pygmy marmoset	Primate	VU	Appendix II	Western Amazon Basin in South America	0	0	0	0	1	5	6	3,4
Cebus capucinus (Linnaeus, 1758) ∆	White-faced capuchin	Primate	LC	Appendix II	Central America	0	0	0	0	1	2	5	3,75
Chinchilla chinchilla (Lichtenstein, 1829) ∆	Short-tailed chinchilla	Rodentia	EN	Appendix I	South America	15	7	416	3,663	2	5	40	1
Chinchilla lanigera (Molina, 1782) ∆	Long-tailed chinchilla	Rodentia	EN	Appendix I	South America	14	6	400	4,114	2	0	81	1,145
Echinops telfairi (Martin, 1838) ∆	Lesser hedgehog tenrec	Afrosoricida	LC	Non-CITES	Southern and south-western Madagascar	9	4	117	3,275	3	2	8	1,55
Meriones unguiculatus (Milne-Edwards, 1867) ∆	Mongolian gerbil	Rodentia	LC	Non-CITES	Mongolia and north-eastern China	10	5	213	196	2	4	8	131

Scientific name	Common name	Order	IUCN	CITES status	Native origin	Pet shop				Online			
						No. of pet shops	No. of SA provinces	Total no. of individuals advertised	Mean price (ZAR)	No. of websites	No. of SA provinces	Total no. of individuals advertised	Mean price (ZAR)
Mesocricetus auratus (Waterhouse, 1839)	Golden hamster	Rodentia	VU	Non-CITES	Syria, southeast Europe and Asia Minor	54	8	1,195	188	3	5	81	46
Mus musculus (Linnaeus, 1758)* ∆	House mouse	Rodentia	LC	Non-CITES	Eurasia	68	8	1,368	43	2	7	125	9
Mustela putorius furo (Linnaeus, 1758)	Domesticated ferret	Carnivores	NE	Non-CITES	Western Eurasia and North Morocco	2	2	52	3,275	2	4	41	1,538
Octodon degus (Molina, 1782)	Common degu	Rodentia	LC	Non-CITES	Central Chile	18	5	385	733	1	5	60	218
Oryctolagus cuniculus (Linnaeus, 1758)*	European rabbit	Lagomorphs	EN	Non-CITES	South-western Europe and to northwest Africa	101	8	6,17	370	3	8	1 195	230
Petaurus breviceps (Waterhouse, 1838)	Sugar glider	Diprotodontia	LC	Non-CITES	Australia and New Guinea	3	1	75	2,588	3	7	132	2,329
Phodopus sungorus (Pallas, 1773)	Winter white dwarf hamster	Rodentia	LC	Non-CITES	Southwest Siberia, eastern Kazakhstan and Khakassia Russia	59	8	2,052	202	3	6	155	63
Potos flavus (Schreber, 1774)	Kinkajou	Rodentia	LC	Appendix III	Central America Bolivia, south-eastern Brazil	0	0	0	0	2	2	39	6,6
Rattus norvegicus (Berkenhout, 1769)*	Norwegian rat	Rodentia	LC	Non-CITES	Eurasia	78	8	3,195	175	4	5	262	60

Scientific name	Common name	Order	IUCN	CITES status	Native origin	Pet shop				Online			
						No. of pet shops	**No. of SA provinces**	**Total no. of individuals advertised**	**Mean price (ZAR)**	**No. of websites**	**No. of SA provinces**	**Total no. of individuals advertised**	**Mean price (ZAR)**
Saguinus midas (Linnaeus, 1758) Δ	Red-handed tamarin	Primate	LC	Appendix II	Brazil, Guyana, French Guiana, and Surinam	0	0	0	0	1	1	8	8
Saguinus oedipus (Linnaeus, 1758) Δ	Cotton-top tamarin	Primate	CE	Appendix I	Northwest Colombia	0	0	0	0	1	1	5	12
Saimiri sciureus (Linnaeus, 1758)	Common squirrel monkey	Primate	LC	Appendix II	South America	0	0	0	0	1	1	14	5
Sciurus carolinensis (Gmelin, 1788)* Δ	Eastern grey squirrel	Rodentia	LC	Non-CITES	Eastern North America	0	0	0	0	1	2	6	3,25
Vulpes zerda (Zimmermann, 1780)	Fennec fox	Carnivora	LC	Appendix II	North Africa, the Sinai Peninsula, South-East Egypt and the Arabian desert	0	0	0	0	2	2	32	4,5

Appendix I: comprises of species threatened with extinction and the trade in specimens of these species is permitted only in exceptional conditions (https://www.cites.org/eng/disc/how.php)
Appendix II: includes species that are not threatened with extinction, but trade in specimens of these species must be controlled (https://www.cites.org/eng/disc/how.php)
Appendix III: includes protected species in at least one country, which has asked other CITES Parties for assistance in controlling the trade (https://www.cites.org/eng/disc/how.php)

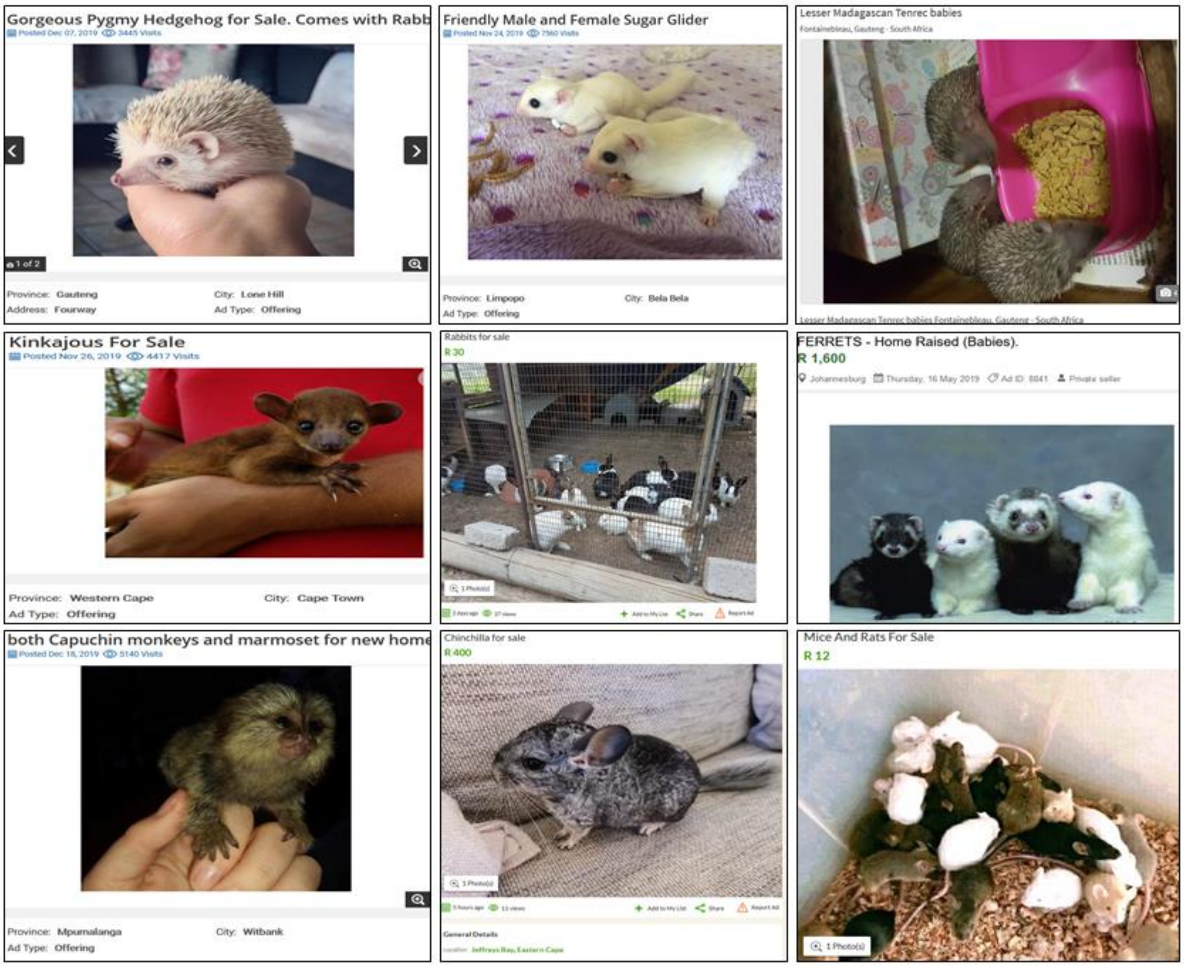
Supplementary material Table S2.3 Non-native small mammals reported being invasive elsewhere and in South Africa. Introduction pathway is the pathway in which the species were introduced, and references are provided.

Scientific name	Common name	Countries invaded	Invasion pathway	References
Callithrix jacchus	Common marmoset	South, Southeast and Northeast Brazil	Release and escape (pet)	Rylands et al. (2008), da Rosa et al. (2017)
Callithrix penicillata	Black-tufted ear marmoset	Southeast Brazil	Release and escape (pet)	Rylands and Mendes (2008), da Rosa et al. (2017)
Mus musculus	House mouse	All continents except Antarctica	Accidental escape (hitch-hikers on trading ships and cargos)	Long (2003), Measey et al. (2020)
Mustela putorius furo	Domesticated ferret	Europe: Azores, United Kingdom and New Zealand	Intentional releases and accidental escape (pet, hunting, fur farming)	Buckley et al. (2007), Long (2003)
Oryctolagus cuniculus	European rabbit	All continents	Intentional release and accidental escape (food or farming)	Long (2003), Braysher (2017),Measey et al. (2020)
Petaurus breviceps	Sugar glider	Tasmania	Accidental escape (pet)	Gunn (1846), Heinsohn (2004)
Rattus norvegicus	Norwegian rat	All continents except Antarctica	Accidental escape (hitch-hikers on trading ships and cargos), release and escape (pets)	Svihla (1936), Long (2003), Measey et al. (2020)
Saimiri sciureus	Common squirrel monkey	Rio de Janeiro State, Brazil	Release (pet)	Camarotti et al. (2015), da Rosa et al. (2017)
Sciurus carolinensis	Eastern grey squirrel	South Africa, Europe: Ireland, Italy and the United Kingdom, North America: Columbia, Australia: Pitcairn	Intentional release and accidental escape (pet, ornamentation)	Long (2003), Huynh et al. (2010), Measey et al. (2020)

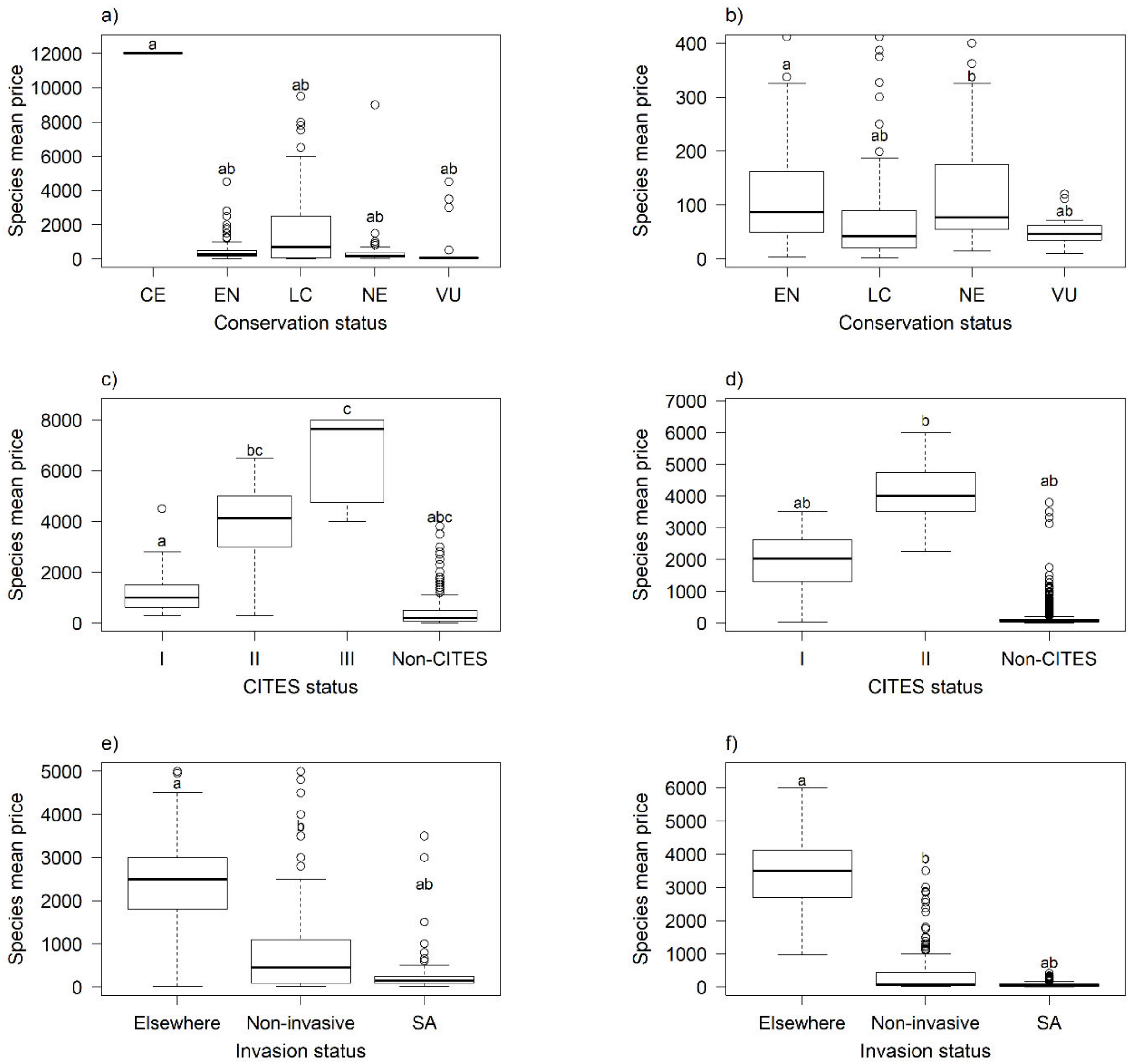
Supplementary material Table S2.4 The regression models for each predictor variable showing the relationship between the log-transformed price and numbers of non-native small mammal species traded as pets in South Africa.

Online trade	**Model**	**Estimates (β)**	**Std. Error**	**t-value**	**P-value**	**AIC**
CITES	Price ~ number + Appendix I	1.55	0.18	8.51	<0.01	107.99
	Price ~ number + Appendix II	-0.22	1.23	-0.18	0.86	70.45
	Price ~ number + Appendix III	-5.06	5.05	-1.0	0.35	13.76
	Price ~ number + non-CITES	1.98	0.13	14.88	<0.01	1388.9
Conservation Status	Price ~ number + NE	-0.56	0.47	-1.15	0.25	146.79
	Price ~ number + VU	1.80	0.41	4.32	<0.01	69.45
	Price ~ number + LC	1.80	0.13	13.42	<0.01	649.42
	Price ~ number + EN	2.97	0.29	9.93	<0.01	729.76
Invasion status	Price ~ number + invasive elsewhere	2.36	0.20	14.35	<0.01	942.99
	Price ~ number + invasive in SA	2.42	0.30	9.23	<0.01	738.1
	Price ~ number + non-invasive	1.23	0.15	8.18	<0.01	605.32
Physical pet shops	**Model**	**Estimates (β)**	**Std. Error**	**t-value**	**P-value**	**AIC**
CITES	Price ~ number + Appendix I	6.86	0.16	41.95	<0.01	49.04
	Price ~ number + Appendix II	0.15	0.22	0.69	0.49	24.33
	Price ~ number + non-CITES	-1.40	0.12	-11.73	<0.01	1222.7
Conservation Status	Price ~ number + NE	0.06	0.07	0.87	0.38	-17.51
	Price ~ number + VU	-0.15	0.09	-1.67	0.09	13.63
	Price ~ number + LC	0.39	0.05	7.32	<0.01	714.98
	Price ~ number + EN	4.71	0.09	54.75	<0.01	411.54
Invasion status	Price ~ number + invasive elsewhere	5.61	0.09	59.17	<0.01	767.32
	Price ~ number + invasive in SA	6.64	0.07	92.92	<0.01	356.32
	Price ~ number + non-invasive	4.21	0.11	39.69	<0.01	547.19

Supplementary material Figure S2.1 Examples of non-native and native small mammal species sold as pets in South Africa. Pictures were taken from different pet shops in the present study (©photograph N Shivambu).



Supplementary material Figure S2.2 Examples of non-native small mammal species sold as pets in South Africa. Pictures were taken from different advertising websites in the present study (©photograph Gumtree, PublicAds).



Supplementary material Figure S2.3 Mean prices for 24 small mammal pets in South Africa based on conservation status, CITES and invasion status for online (a, c, and e) and pet shops (b, d, and f). Letters i, ii, and iii indicate CITES-listed Appendices. For invasion status, "Elsewhere" = invasive elsewhere and "SA" = invasive in South Africa. The same letters indicate significant differences between the groups based on Mann-Whitney pairwise test; $P < 0.001$, Bonferroni corrected p values.

CHAPTER 3

A survey of non-native small mammals traded in South Africa: Pet shop owners' perceptions

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3.1 Abstract

The sale of live non-native animals has become a social norm and is of global concern as some of these species become invasive and/ or endangered. Pet trade has become one of the main pathways whereby live non-native small mammals are introduced worldwide. We conducted a survey questionnaire in South African pet shops from September 2018 to September 2019 to determine the species composition across the pet shops across provinces and recorded small mammalian species sold. We also investigated if the pet shop owners were aware of the South African National Environmental Management: Biodiversity Act (NEM: BA), which regulates and provides management and conservation of the country's biodiversity. A total of 111 pet shop owners/ managers responded to the survey, with 26.6% of the owners reporting the sale of birds, 25.1% fish and 22.5% mammals. A total of 16 non-native small mammalian species were reported sold, with European rabbit (*Oryctolagus cuniculus*), Norwegian rat (*Rattus norvegicus*), and house mouse (*Mus musculus*) being the most commonly sold pets. Most respondents acquired their non-native small mammals from breeders, followed by animal rescues and pet shops. Most respondents (67.8%) were aware of NEM: BA. Therefore, we recommend that government regulating bodies engage with the pet trade industry and the general public and pet shop owners to assist in preventing the introduction of potentially invasive pets in South Africa.

Keywords: Pet trade; invasion pathways; regulations; risk; escape; release; prohibited species

3.2 Introduction

Non-native animals have been and continue to be introduced in South Africa through various pathways including stowaway, biological control, scientific research, food, zoo and pet trade (Faulkner et al., 2020; Measey et al., 2020; Moshobane et al., 2020). The pet trade industry is growing in South Africa, and reptile, small mammal, amphibian, mollusc and invertebrate species are being sold (van Wilgen, Richardson, & Baard, 2008; Maligana et al., 2020; Nelufule et al., 2020; Shivambu et al., 2020a, b, c). Some non-native species have established feral populations (i.e. species once domesticated but now living in the wild) through pet trade releases and escapes around the world (da Rosa et al., 2017; Lockwood et al., 2019; Shivambu et al., 2020a, 2021). Understanding the role of the pet trade in facilitating invasions is essential in preventing potential impacts associated with them (Shivambu et al., 2021).

Most of the companion/pet species are acquired by individuals from pet expos, breeders, online trade, and/ or pet shops (Meenken, 2012; Halsby et al., 2014; Kelso, 2018; Nelufule et al., 2020; Shivambu et al., 2021). Recent studies on the pet trade have focussed on online trade and pet shops as the main source of introduction for live non-native pets (Mahmood et al., 2011; Su et al., 2015; Lockwood et al., 2019; Nelufule et al., 2020; Shivambu et al., 2021). These two sources are relatively easy to study and are more accessible as opposed to accessing private breeders or pet expos for information (Maligana et al., 2020; Nelufule et al., 2020). The majority of pet shops globally and in South Africa are located in urban areas, especially large cities and are often found in shopping malls (Soorae et al., 2008; Mahmood et al., 2011; Shivambu et al., 2020a, b). These shops sell different types of non-native pets, including amphibians, reptiles, birds, aquatic organisms and small mammals (Soorae et al., 2008; Mahmood et al., 2011; Warwick et al., 2018; Maligana et al., 2020; Nelufule et al., 2020; Shivambu et al., 2020c). Small mammals such as Norwegian rats (*Rattus norvegicus*), mice (*Mus musculus*, *Mastomys coucha*), guinea pigs (*Cavia porcellus*), hamsters (*Phodopus* *roborovskii*, *Mesocricetus auratus*) and European rabbits (*Oryctolagus cuniculus*) are sold in various physical pet and online shops in South Africa and globally (Mclaughlin & Strunk, 2016; Lankau et al., 2017; Kelso, 2018; Maligana et al., 2020; Shivambu et al., 2020c).

The trading of these non-native pets has since been criticised by the public health, animal welfare and species conservation authorities (Warwick et al., 2018, 2021; Spee et al., 2019). Public health research indicates that non-native pets are responsible for transmitting zoonotic diseases to humans, where for example, small mammals are reservoirs for pathogens that cause diseases such as COVID-19, rat-bite fever, cowpox, and ringworm which are fatal to humans (Chomel et al., 2006; Smith, Smith, & Auria, 2012; Warwick et al., 2012; Kiros et al., 2020). Animal welfare concerns have been raised as often these pets suffer during transportation or when captured, breeding and housing (Ashley et al., 2014; Grant, Montrose, & Wills, 2017). Species conservation research highlights that several non-native species may become invasive, while native species may become endangered as a result of individuals being removed from the wild in their native ranges (Bush, Baker, & Macdonald, 2014; Warwick et al., 2018). Consequently, different countries have developed legislation to regulate the trade of some of the non-native animals (Stoakes, 2014; Spee et al., 2019).

In South Africa, non-native species are regulated under the South African National Environmental Management: Biodiversity Act (No. 10 of 2004) (NEM: BA), which group species into four categories, namely, category 1a, category 1b, category 2 and category 3 (DEA, 2016). Relatively few non-native small mammal pets are prohibited from being imported into South Africa under these regulations. For example, currently, the European hedgehogs (*Erinaceus europaeus*), short-tailed weasels/stoats (*Mustela ermine*), and brushtail possums (*Trichosurus vulpecula*) cannot be imported (DEA, 2016). Popular small mammals in the South African pet trade such as Norwegian rats, house mice (*M. musculus*) and European rabbits are listed as category 1b for South African offshore islands (DEA, 2016; Shivambu et al., 2020c, 2021). According to the regulations, these three species may not be owned, imported, moved, sold and given as a gift, but this applies only to the South African offshore islands. There are currently no regulations that prevent the selling, importing or breeding of these three invasive species in mainland South Africa.

Rats and mice are also sold in pet shops as feeders for other pets, such as snakes in South Africa and other countries (Lee et al., 2008; Harker et al., 2011; Cooper & Williams, 2014; Kanagarajah et al., 2018; Maligana et al., 2020). Pet shops do not just sell these non-native pets; they have to apply for a permit to trade some of these species (Drews, 2001; Stoakes, 2014; Su et al., 2015). Pet shops are also highly regulated and are always under inspection; consequently, they offer few different non-native pets when compared with the online trade (Pasmans et al., 2017; Shivambu et al., 2020c; 2021). In South Africa, approximately 42 pet shops are registered with the South African Pet Traders Association (SAPTA), and only 19 of these sell non-native small mammals (SAPTA, 2019). Given this background, the present study investigated: 1) species composition across the provinces and which small mammalian species were sold; 2) the sources from where pet shops acquire their non-native small mammals; and 3) if the pet shops were aware of the regulations which govern the sale of non-native pets. We predicted that rodents would be the most popular species traded because they are relatively easy to maintain, are cheaper, and are often sold as feeders for reptiles such as snakes (Maligana et al., 2020; Shivambu et al., 2021). We also predicted that pet shop owners acquire their pets from different sources.

3.3 Methods

3.3.1 Questionnaire survey

We compiled a list of pet shops selling non-native animals in South Africa using the South African Pet Traders Association (SAPTA) (http://www.sapettraders.co.za/), and pet shop directory (http://www.pet-shops.co.za/) websites. An additional list was compiled by searching for pet shops on Google earth (https://earth.google.com/web/) and maps (https://www.google.co.za/maps) using phrases such as "pet shops in South Africa" or "list of pet shop names in South Africa". A total of 121 pet shops across South Africa were visited during the parallel study (Shivambu et al., 2021). We conducted an opportunistic survey to gather information about the species traded. During our first visit, we collected email addresses and advertising websites of all the visited pet shops. We provided the pet owners or workers with information about our study, including an explanation about the NEM: BA regulations, trading of native and endangered species.

The survey questionnaire was developed using Google forms (https://www.google.com/forms/about/). The survey consisted of 17 questions, of which seven were multiple-choice, eight checkboxes and two were fill-in (https://goo.gl/forms/in1C2zlyawJctMUg2; Supplementary Material Table S3.1). The survey questions were designed to collect information on which non-native animals are sold in South Africa. However, small mammals formed the main focus of this study. The first page of the survey had a short paragraph describing the study. Permission to conduct the survey questionnaire was granted by the University of KwaZulu-Natal - Humanities and Social Research Ethics Committee (Protocol number: HSS/0908/018D). The survey data were collected based on two methods, online and face to face interviews. The online survey remained active for a year, from September 2018 to September 2019. Of the visited pet shops, 89 responded to an online version, while 22 responded to the paper-based survey during the follow-up survey for the parallel study (Shivambu et al., 2021). Ten pet shops did not allow us into their premises, and nine refused to participate in the survey questionnaire.

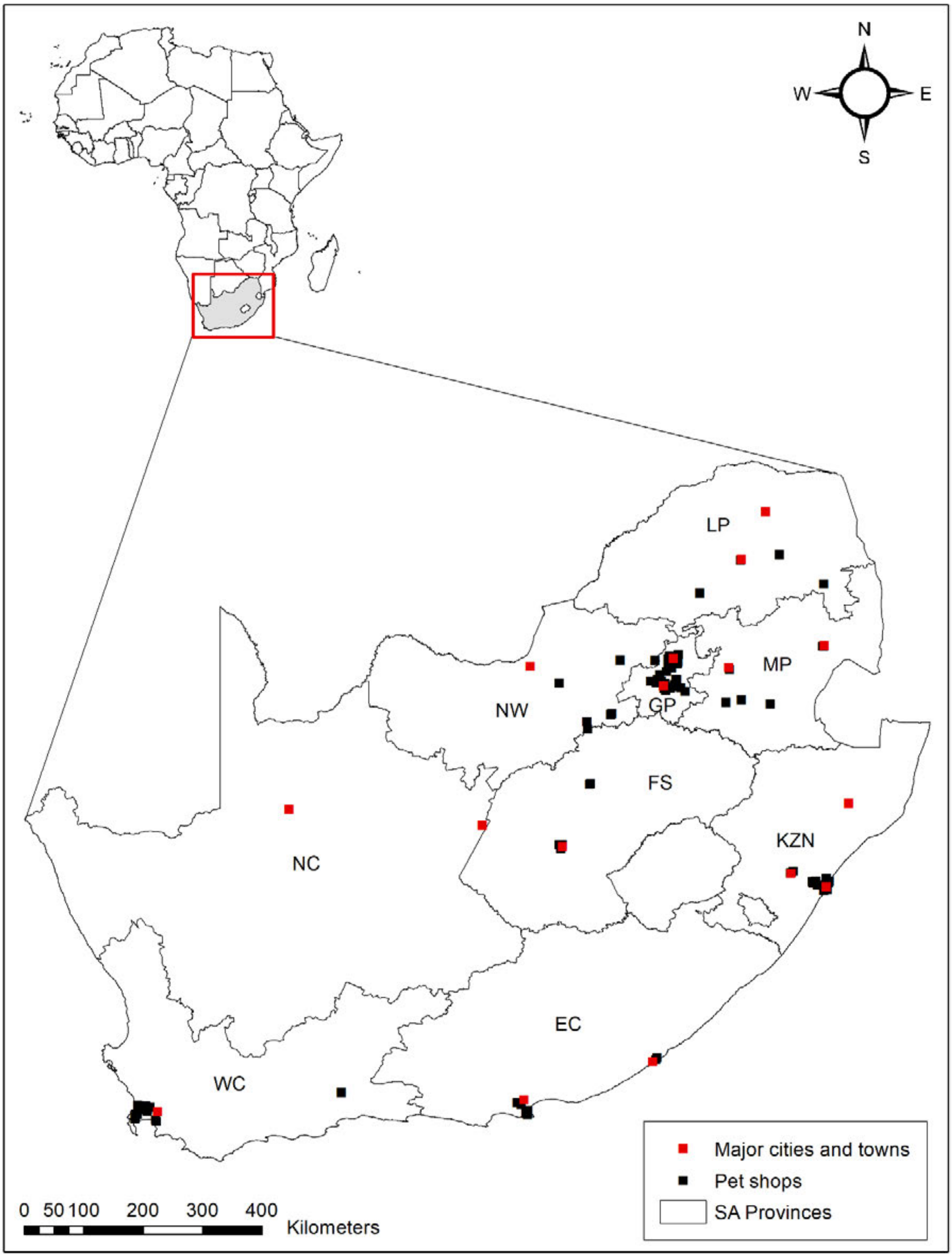

Fig. 3.1 A map of South Africa showing the physical pet shop locations surveyed between September 2018 to September 2019 in the respective provinces. Each Province is denoted by the following letters EC – Eastern Cape, FS – Free State, GP – Gauteng Province, KZN – KwaZulu-Natal, LP – Limpopo Province, MP – Mpumalanga Province, NW – North West, NC – Northern Cape, and WC – Western Cape.

3.3.2 Statistical analyses

To determine if data were normally distributed, identical, and independent, we used the Kolmogorov-Smirnov normality test (Lilliefors, 1967). We found that the data were not normally distributed; therefore, a Kruskal-Wallis test by ranks (Kruskal and Wallis 1952) was used to test for the differences between the number of respondents. We further used the Mann-Whitney pairwise test (Mann and Whitney 1947) with Bonferroni p values adjusted at 0.01 to determine the significant difference between the number of respondents. The Mann-Whitney pairwise test was also used to determine the difference between species composition across the provinces. The responses were grouped by province for statistical analyses. All statistical analyses were based on algorithms in R Studio statistical analysis software packages, version 3.6.3 (R Core Team, 2018).

3.4 Results

3.41 Number of survey questionnaire respondents

A total of 111 pet shop owners responded to the survey. However, we could only analyse the results from 107 responses because of some incomplete responses. We found that most of the respondents were from Gauteng Province (sample size (n) = 38, 35.5%), followed by KwaZulu-Natal (n = 20, 18.7%) and Western Cape (n = 17, 15.9%) Provinces (Supplementary Material Table S3.2). Most of the respondents in Gauteng Province considered that their province has between 50 and 80 pet shops, while respondents from KwaZulu-Natal and Western Cape Provinces considered that their provinces have ~20 and ~40 pet shops, respectively (Supplementary Material Table S3.2). Respondents from the remaining six provinces in South Africa considered that they have between one and 10 pet shops (Supplementary Material Table S3.2).

3.4.2 Species traded in South African pet shops

In the present study, seven major animal groups were recorded to be traded in the South African pet shops (Fig. 3.2). Respondents showed that birds (*n* = 103, 26.6%), fish (*n* = 97, 25.1%) and mammals (*n* = 87, 22.5%) were the most animal groups sold by pet shops when compared with other animal groups (Kruskal-Wallis test by ranks: χ^2 = 26.77; df = 6; *n* = 386; *P* = 8.43e-05) (Supplementary Material Table S3.2). About 17.3% (*n* = 67) of the pet shop respondents indicated that they sold reptiles, while 3.8% (*n* = 15) amphibians, and 2.9% (*n* = 10) sold arthropods (Fig. 3.2; Supplementary Material Table S3.2). The other groups such as molluscs, insects and invertebrates were traded by less than 2% (*n* = 7) of the pet shops (Fig. 3.2; Supplementary Material Table S3.2).

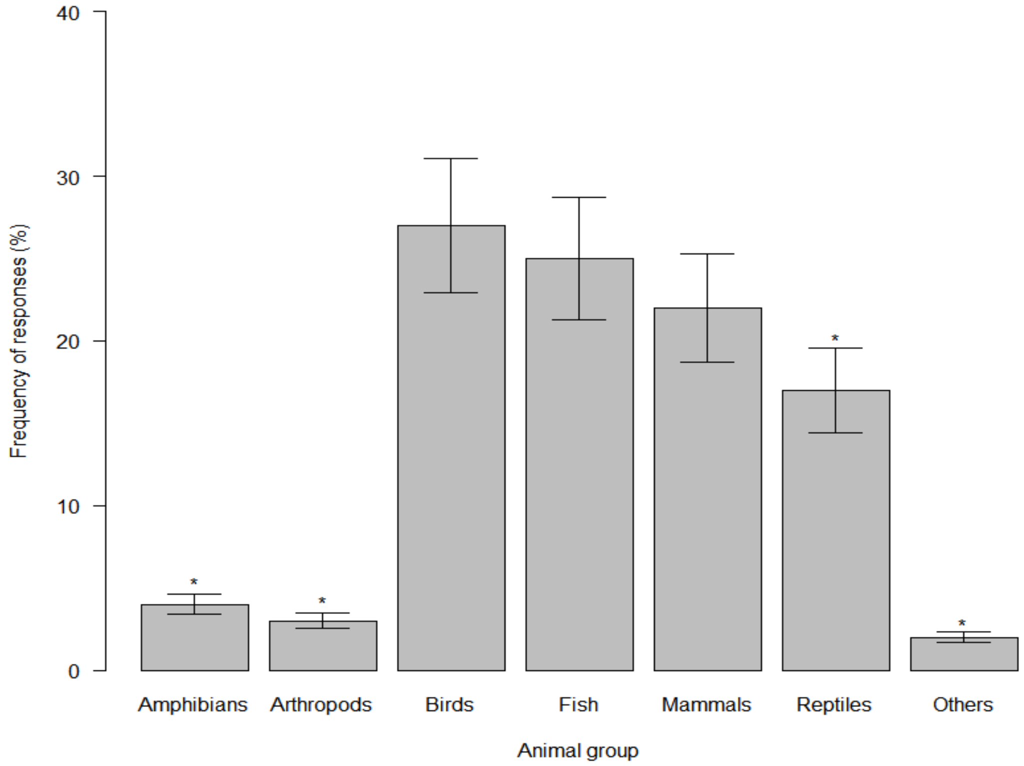

Fig. 3.2 The range of non-native animal groups indicated to be sold by pet shop owners in South Africa in the present study (n = 386). (An asterisk (*) indicates statistical significance at $P < 0.01$).

A total of 16 small mammalian species were reported to be traded by 89 pet shops (Fig. 3.3; Supplementary Material Table S3.2). The most-traded small mammalian species were European rabbit (*Oryctolagus cuniculus*; n = 76, 16.2%), Norwegian rat (*Rattus norvegicus*; n = 72, 15.4%), house mouse (*Mus musculus*; (n = 65, 13.9%), guinea pig (*Cavia porcellus*; n = 63, 13.5%), golden hamster *Mesocricetus auratus* (n = 38, 8.1%) and winter white dwarf hamster *Phodopus sungorus* (n = 13, 2.8%) (Fig. 3.3; Supplementary Material Table S3.2). There were significantly higher percentages of respondents who traded in these species than other small mammalian species sold (Kruskal-Wallis test by ranks: χ^2 = 42.60; df = 15; n = 468; P = 1.52e-05) (Supplementary Material Table S3.2). The short-tailed chinchilla (*Chinchilla chinchilla*), long-tailed chinchilla (*C. lanigera*), common degu (*Octodon degus*), Mongolian gerbil (*Meriones unguiculatus*), sugar glider (*Petaurus breviceps*), four-toed hedgehog (*Atelerix albiventris*) and lesser hedgehog tenrec (*Echinops telfairi*) were not commonly sold (Fig. 3.3; Supplementary Material Table S3.2). The least popular non-native small mammals traded were eastern grey squirrel (*Sciurus carolinensis*), domesticated ferret (*Mustela putorious furo*) and common marmoset (*Callithrix jacchus*) (Fig. 3.3; Supplementary Material Table S3.2).

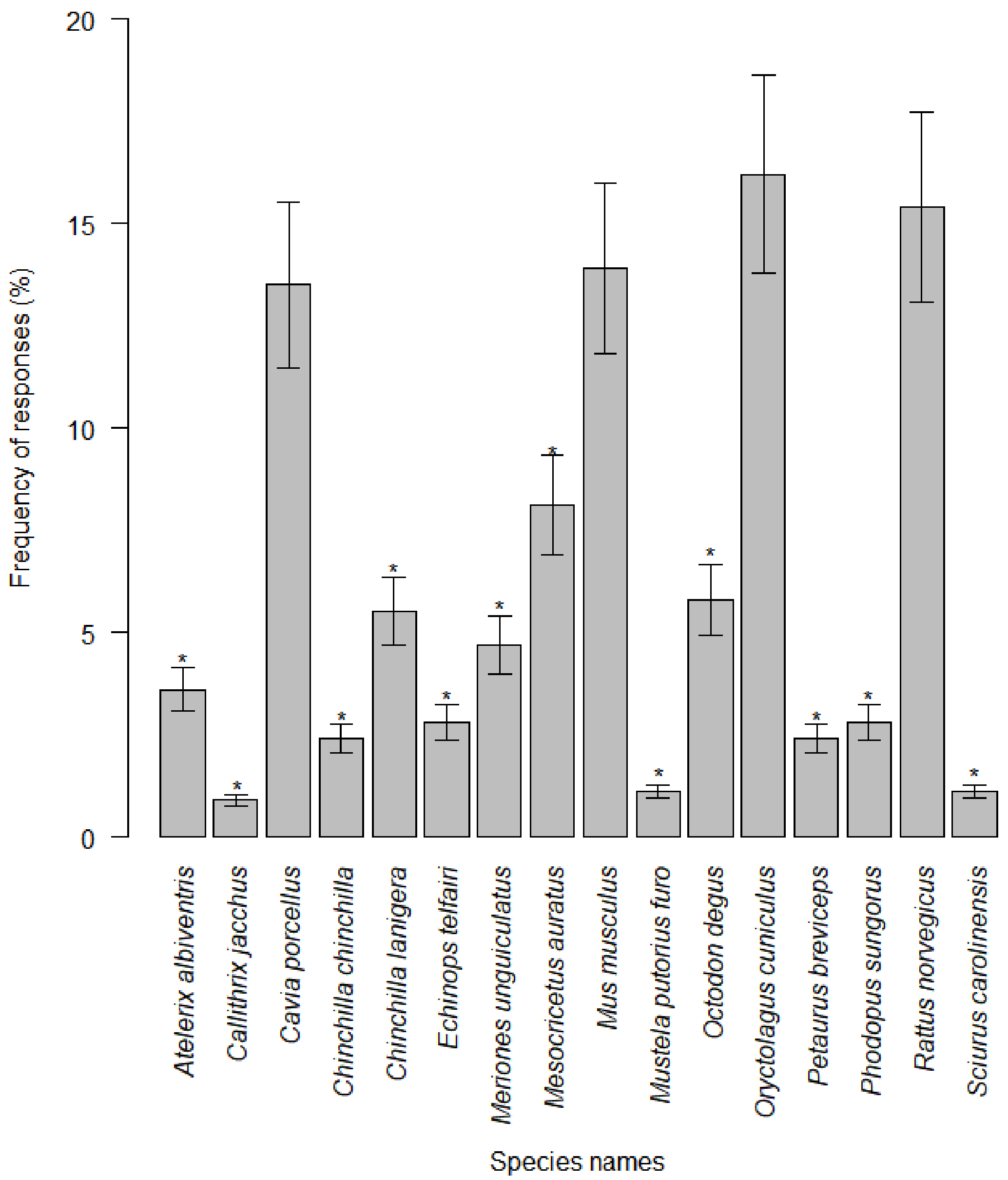

Fig. 3.3 Non-native small mammals indicated to be sold by pet shop owners in South Africa in the present study (n = 468). (An asterisk (*) indicates statistical significance at $P < 0.01$).

Our results showed that mammalian species composition traded differed across the South African provinces (Kruskal-Wallis test by ranks: $\chi^2 = 55.78$; df = 8; n = 468; P = 4,87e-10) (Supplementary Materials Table S3.2). Gauteng Province had a significantly higher species composition than other provinces, representing 46% (n = 216) of species (Mann-Whitney pairwise test; $P < 0.001$, Bonferroni corrected P-values) (Table 3.1). This was followed by

KwaZulu-Natal Province, which represented 20% (n = 94) of species composition. Species composition for North West (n = 42) and Western Cape (n = 40) was similar, both representing 9% of species (Table 3.1). Other provinces represented less than 6% of the total species composition. Our results also showed that Gauteng had high species richness, with all the recorded species in the country sold in the province (Table 3.1). This was followed by KwaZulu-Natal, North West, and Western Cape Provinces, of which 13 species were traded in by the first two provinces and 12 by the latter (Table 3.1). Respondents from the other five provinces indicated to sell less than 10 species (Table 3.1).

Table 3.1 Mann-Whitney pairwise test comparison of species composition between provinces based on the number of responses (*n* = 486).

Provinces	**EC**	**FS**	**GP**	**KZN**	**LP**	**MP**	**NW**	**NC**	**WC**	**Species composition**	**Species richness**
EC		1	7.14e-05**	0.04*	1	1	0.28	1	0.94	11	7
FS	1		0.00**	0.27	1	1	1	1	1	24	7
GP	7.14e-05**	0.00**		0.69	0.00**	3.39e-05**	0.00**	6.70e-05**	0.00**	216	16
KZN	0,03*	0.27	0,69		0.32	0.01*	1	0.04*	1	94	13
LP	1	1	0.00**	0.32		1	1	1	1	24	7
MP	1	1	3.39e-05**	0.01*	1		0.03*	1	0.11	6	4
NW	0.28	1	0.00**	1	1	0.03*		0.29	1	42	13
NC	1	1	6.70e-05**	0.04*	1	1	0.29		1	11	8
WC	0,94	1	0.00**	1	1	0.11	1	1		40	12

**Represent level of significance below 0.01, *represent level of significance below 0.05
The abbreviations denote each Province, EC – Eastern Cape, FS – Free State, GP – Gauteng Province, KZN – KwaZulu-Natal, LP – Limpopo Province, MP – Mpumalanga Province, NW – North West, NC – Northern Cape, and WC – Western Cape.

3.4.3 Sources of trade

According to the respondents in the present study, non-native small mammalian species in the pet trade in South Africa were generally obtained from a range of different sources. We found that there was a significant difference between the sources of these species (Kruskal-Wallis test by ranks: $\chi^2 = 17.58$; df = 6; $n = 197$; $P = 0.00$) (Fig. 3.4; Supplementary Material Table S3.2). Most of the pet shop owners indicated that they obtained their small mammal pets from specific breeders ($n = 67$, 34.0%). Between 10% and 16% of respondents indicated that they acquired their pets for trade from animal rescues ($n = 31$, 15.7%), other pet shops ($n = 27$, 13.7%), overseas trade ($n = 25$, 12.7%), online trade ($n = 24$, 12.2%) and others bred their pets to sell (i.e., self-bred; ($n = 20$, 10.2%) (Fig. 3.4; Supplementary Material Table S3.2). Only 1.5% ($n = 3$) of the respondents indicated that they acquired their pets for trade from the wild (Fig. 3.4; Supplementary Material Table S3.2).

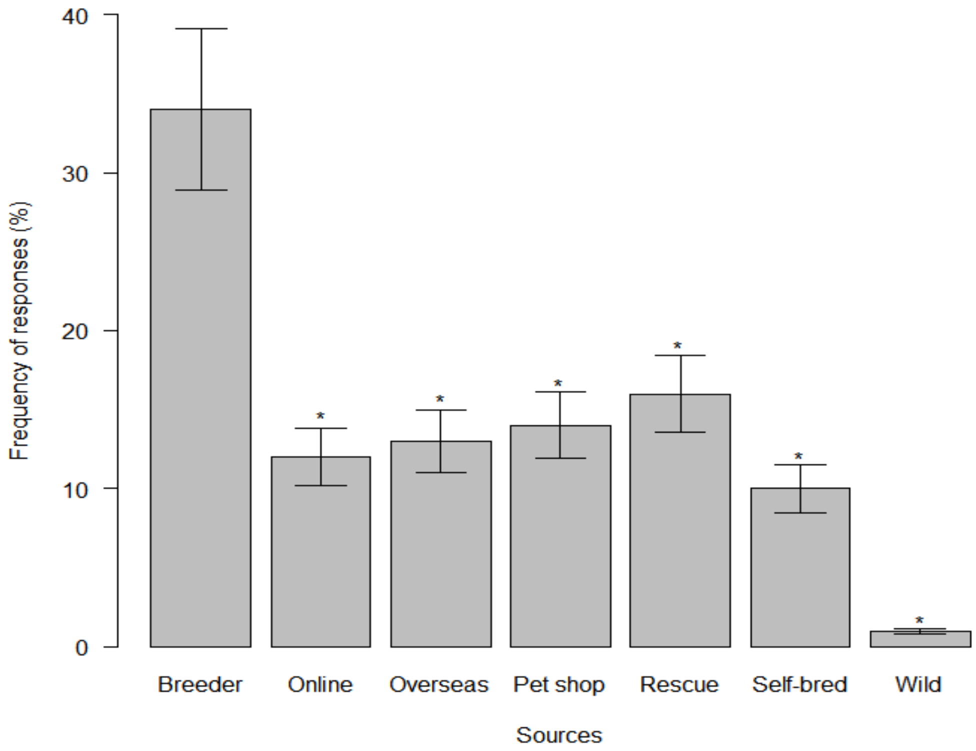

Fig. 3.4 List of sources from where pet shop owners in South Africa acquired their non-native small mammalian species in the present study (*n* = 197). (An asterisk (*) indicates statistical significance at $P < 0.01$).

3.4.4 Trends in sales and South African National Environmental Management: Biodiversity Act (NEM: BA)

A total of 37.0% (number of pet shop owners (*n*) = 33) indicated an increase in the sale of small mammalian species between 2000 and 2017. This was attributed to reasons such as high demand, affordable prices, and the relative ease to maintain small mammalian species (Supplementary Material Table S3.2). Those who indicated that their sales were not increasing indicated that NEM: BA regulations were the main reason, followed by competition with other pet shops, and other reasons included that people are afraid of zoonotic diseases (Supplementary Materials Table S3.2). About 49.4% (*n* = 43) of pet shop owners indicated that small mammals made a small percentage of their sales. In comparison, 50.6% (*n* = 44) indicated that small mammals did not make a small percentage of their sales. When asked if they will continue to sell, 89.1% (*n* = 51) indicated that they would continue to sell small mammalian species (Supplementary Materials Table S3.2).

Our results showed that there was a significant difference between those who were aware (*n* = 59, 67.8%) of NEM: BA regulations and those who were not (*n* = 28, 32.2%) (Kruskal-Wallis test by ranks: χ^2 = 14.31; df = 1; *n* = 87; *P* = 0.02) (Supplementary Material Table S3.2). A total of 71.3% (*n* = 62) of respondents were against the small mammal trade to be regulated, while 28.7% (*n* = 25) agreed with the regulation. Respondents who indicated that the sale of small mammals should be regulated suggested that firm regulations should be developed, fines should be imposed on those who broke the law, and illegal traders should be arrested (Supplementary Material Table S3.2). Some respondents indicated that imports of small mammalian species should be strictly controlled. However, respondents who showed that the sale of small mammals should not be regulated argued that the pet trade industry forms part of the economy and promotes animal conservation responsibility (Supplementary Material Table S3.2). A total of 57.5% (*n* = 50) of pet shop owners indicated that they lose individuals of small mammalian species through escapes, while 42.5% (*n* = 37) showed that they do not lose them (Supplementary Material Table S3.2). However, those who showed that they lose small mammalian species as escapes also indicated that most mammals are re-captured as they escape into a closed environment.

3.5 Discussion

The pet trade industry is growing in South Africa, and the pet shop is one of the top avenues where non-native pets are introduced (van Wilgen et al., 2008; Maligana et al., 2020; Nelufule et al., 2020; Shivambu et al., 2020a, b, c, 2021). Consequently, species introduced through this avenue should be documented, as non-native pets may potentially become invasive through accidental escapes and intentional releases (da Rosa et al., 2017; Shivambu et al., 2021). Our study showed that Gauteng, Western Cape and KwaZulu-Natal Provinces have the most pet shops selling non-native pets. These three provinces are among the fastest-growing economies in South Africa, and the relatively high number of pet shops may be explained by the economic status of these provinces (Shivambu et al., 2021). In addition, the species composition for these three provinces was high. However, even though KwaZulu-Natal Province had more pet shops and high species composition, its species richness was similar to that of North West Province, which had few pet shops. This may suggest that species composition and richness are not correlated to the number of pet shops (Shivambu et al., 2021).

The number of respondents who have pet shops selling non-native pets in our study may underestimate the total number of pet shops in South Africa. For example, most of the respondents in Gauteng Province indicated that they have between 50 and 80 pet shops. This number is lower than the number of pet shops surveyed in the province, indicating that some of the pet shops may not be registered or only operate online with private sellers. This is because most of the pet shops are not registered with organisations such as the South African Pet Traders Association (SAPTA). A study by Martin and Coetzee (2011) on aquatic macrophytes reported that various private vendors and traders who sell different non-native species are not registered with any organisation. As a result, a large number of unregistered vendors may pose a challenge for biodiversity law enforcement, making it challenging to regulate which species enter the country and in what quantities.

Our study reported a total of nine species groups of non-native animals in the trade, and this showed that there are different species introduced as part of the pet trade in South Africa. As a result, this warrants further investigation to determine which species from the reported groups are being traded. Although small mammalian species were found to be the third-most traded group in our study, they were traded in all the provinces in South Africa. In addition, the most commonly traded small mammals were European rabbit, winter white dwarf hamster, golden hamster, Norwegian rat, house mouse and guinea pig. Overall, rodents were the most frequently traded pets when compared with other non-native small mammalian species. The popularity of rodents may be because most are relatively easy to maintain and are often traded as feeders for reptiles (e.g., rats, hamsters and mice; Cooper & Williams, 2014; Kanagarajah et al., 2018; Maligana et al., 2020). Pet shops owners tend to sell pet species that are more popular than rare species (Shiau et al., 2006; Shivambu et al., 2021). Rodents, for example, were indicated to be sold by all the respondents in our study, showing that they are available in most provinces and pet shops. Consequently, the most popular species are most likely to escape or released from captivity when compared with the least popular species (Macdonald, Harrington, & Newman, 2017).

A parallel study by Shivambu et al. (2020c, 2021) found that the most popular species in both pet shops and online trade were the European rabbit, house mouse, Norwegian rat, guinea pig, winter white dwarf hamster and golden hamster. We suggest that the sale of these species should be monitored and managed to prevent invasions and potential impacts, as reported by Shivambu et al. (2020c). However, pet shop owners have neither control over who they sell their pets to, nor do they know if their clients will release the species or not. This indicates that education about the potential impacts of non-native pets, in general, is necessary. A large percentage of pet shop owners indicated that species escape enclosures but are later found inside the pet shops. However, this may pose an invasion risk should some of the species escape unnoticed as many mammalian species can tolerate a wide range of climatic conditions, have high reproductive rate, catholic diets, are commensal, and some lack predators (Clout & Russel, 2007; Latham et al., 2017). In addition, some of the pet owners release their species for reasons such as fear of zoonotic diseases, species becoming aggressive, lack of knowledge regarding the species kept, unwanted pets, and loss of interest in the pets (Padilla & Williams, 2004; Reaser & Meyers, 2007; Secretariat of the CBD, 2010; Stringham & Lockwood, 2018).

For example, rodent species such as Norwegian rats and house mice carry zoonotic diseases that can be transmitted to humans (Lundkvist et al., 2013; Nordholm et al., 2019). As a result, this may lead to intentional releases of these pets.

Breeders were indicated as the most common suppliers for non-native small mammalian species to the South African pet shops. This showed that there are different breeders in the country who supply different small mammalian species to the growing pet trade business. The trade in small mammals is likely to increase given that most of the respondents indicated that they would continue to sell these species, although it makes a relatively small percentage of their sales. In addition, potential invasive small mammals may likely be imported into the country as there were some pet shop owners who indicated that they were not aware of the regulations. Lack of knowledge of regulations was shown as the reason for the introduction of some plant species in South Africa (see Martin & Coetzee, 2009). However, knowledge of regulations does not necessarily indicate that some of the pet shop owners may not import prohibited species. For example, prohibited and invasive amphibians, crayfish and birds were sold in the European Union and Canada despite regulations (Patoka, Kalous, & Kopecký, 2014; Genovesi et al., 2015; Auliya et al., 2016; Faulkes, 2018). This suggests that existing regulations need to be implemented and enforced to prevent the introduction of potentially harmful species. This potential problem may be exacerbated further by the alarmingly large percentage of respondents who opposed the regulating of the non-native small mammal pet trade. However, those who indicated that the species in the pet trade should be regulated, suggested the introduction of firm regulations, enforcing the law, and imposing fines on illegal traders.

Some of the pet shop owners indicated that the pet trade industry creates jobs and forms part of the economy. However, the pet trade industry has some disadvantages, e.g., the European rabbit is critically endangered, yet invasive (Lees & Bell, 2008; Marchetti &

Engstrom, 2016). This species is associated with both environmental and socio-economic impacts (Hagen & Kumschick, 2018; Shivambu et al., 2020c). In addition, small mammalian species pose a health risk to the owners, pet shop workers and the public in general as they are associated with zoonotic diseases that can be transmitted to humans (Mani & Maguire, 2009; Smith et al., 2012; Warwick et al., 2012).

3.6 Conclusions

Our study showed that there are a relatively large number of pet shops selling non-native animals in South Africa, and the provinces with the fast-growing economies had the most pet shops. We, therefore, recommend that pet shops in those provinces be regularly monitored and encouraged to register with the country's pet trader association. This may assist in determining the actual number of pet shops in each province, and therefore they can be easily assessed. As this study reported other animal groups sold by various pet shops, further studies need to determine which other non-native pet species are sold (e.g., fish and bird species). The most popular non-native small mammals were the European rabbit and rodents. Therefore, we recommend that these species be monitored in the pet shops as some of them have potentially high economic and socio-economic impacts (Shivambu et al., 2020c). Specific breeders are the major suppliers for the non-native small mammalian species in the pet shops, and further studies should investigate how many breeders are in South Africa and if they are aware of the regulations related to non-native small mammals. Government regulation authorities need to engage with the pet trade industry, including the general public, regarding the sale of non-native pets to prevent the introduction of potential invasive companion animals/pets. In addition, educating the pet owners about the traits and potential impacts of non-native pets on native biodiversity and society may limit the number of pet owners. We acknowledge some limitations in the present study, including the design of questions that have inhibited our ability to conduct more advanced analyses. As a result, we recommend that future studies should include questions on how the pet trade industry regulations may be improved (see Episcopio-Sturgeon & Pienaar, 2019, 2020). Pet owners should also be engaged in such studies to get their perceptions regarding the trade of non-native species.

3.7 Acknowledgements

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3.8 Conflicts of interest/Competing interests

The authors declare no conflict of interest nor competing interests.

3.9 Authors' contributions

NS and CTD conceptualised and did the sample design. NS implemented the study. NS and TCS analysed the data. NS wrote the manuscript draft while TCS and CTD edited the manuscript before submission.

3.10 Ethics approval

Ethics was approved by the University of KwaZulu-Natal – Humanities and Social Research Ethics Committee (ethic number: HSS/0678/018D).

3.11 Data availability statement

Data for this study is available on request from the authors.

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3.13 Supplementary material

Supplementary Table S3.1 Survey questionnaire for small mammalian species sold in the South African pet shops.

Small mammals survey

We are conducting a study about the sale of exotic small mammals in the South African pet shops. Small mammals are becoming popular as pets in South Africa and for this reason we would like to understand which species of small mammals are being sold in SA and which species are popular. This survey forms part of a PhD degree in Zoology at the university of KwaZulu-Natal. Your participation in this survey is voluntary and it will only take 8 minutes to complete as most of the questions are multiple choice. As pet shop owners or workers, it is important that we hear your opinion regarding this study.

The permission to undertake this survey was given by the university of KwaZulu-Natal Human participation committee. Should you have any questions about the study please contact, Ndivhuwo at ndivhuwomaligana@gmail.com and Prof Downs at downs@ukzn.ac.za
.

Your participation in this survey is very much appreciated.

Thanks!!!!!!

Can you please provide your name and email address (Optional)

Your answer

1. Please indicate your Province

- [ ] Limpopo
- [ ] Gauteng
- [ ] Western Cape
- [ ] Eastern Cape
- [ ] Free State
- [ ] Mpumalanga
- [ ] North West
- [ ] KwaZulu-Natal
- [ ] Northern Cape
- [ ] Other: ____________________

2. Please indicate the number of pet shops you think you have in your province?

- ○ 1
- ○ 2
- ○ 3
- ○ 4
- ○ 5
- ○ Other: ____________________

3. Which non-native animals do you sell in your pet shop?

- [ ] Mammals
- [ ] Reptiles
- [ ] Fish
- [ ] Birds
- [ ] Amphibians
- [ ] Arthropods
- [ ] Other: ____________________

4. Which of these small mammal pets do you sell?

- [ ] Guinea pig (Cavia porcellus)
- [ ] Rat (Rattus norvegicus)
- [ ] Mice (Mus musculus)
- [ ] Rabbit (Oryctolagus cuniculus)
- [ ] Squirrel (Sciurus carolinensis)
- [ ] WInter white dwarf hamster (Phodopus sungorus)
- [ ] Golden hamster (Mesocricetus auratus)
- [ ] Short-tailed chinchilla (Chinchilla chinchilla)
- [ ] Long-tailed chinchilla (Chinchilla lanigera)
- [ ] Gerbil (Meriones unguiculatus)
- [ ] Ferret (Mustela putorius furo)
- [ ] Skunk (Mephitis mephitis)
- [ ] Degu (Octodon degus)
- [ ] Sugar glider (Petaurus breviceps)
- [ ] Prairie dog (Cynomys ludovicianus)
- [ ] Hedgehog (Atelerix albiventris)
- [ ] Tenrec (Echinops telfairi)
- [ ] Common squirrel monkey (Saimiri sciureus)
- [ ] Fennec fox (Vulpes zerda)
- [ ] Cotton-top tamarin (Saguinus oedipus)
- [ ] Red-handed tamarin (Saguinus midas)
- [ ] Kinkajou (Potos flavus)
- [ ] White-faced capuchin (Cebus capucinus)
- [ ] Black tufted-ear marmoset (Callithrix penicillata)
- [ ] Pygmy marmoset (Cebuella pygmaea)
- [ ] Common marmoset (Callithrix jacchus)
- [ ] Other: ____________________

5. Where do you get your small mammals to sell in your pet shop?

- [ ] Pet shop
- [ ] Breeder
- [ ] Online
- [ ] Overseas
- [ ] Wild
- [ ] Rescue
- [ ] Self-bred
- [ ] Other: ______

6. Has there been an increase in the selling of your small mammal pets?

- ○ Yes
- ○ No

7. If yes: since when?

Your answer ______

8. Why do you think the sale is increasing?

- [ ] High demand
- [ ] Affordable prices
- [ ] Other: ______

9. If no, what do you think could be causing the decrease on the sale?

- [ ] Regulations (National Environmental Management: Biodiversity Act No. 10 of 2004)
- [ ] Competition with other pet shops
- [ ] Diseases
- [ ] Species are expensive
- [ ] Other: ____________________

10. Do you know about the National Environmental Management: Biodiversity Act No. 10 of 2004?

○ Yes

○ No

11. Are the small mammals sold a small percentage of your sales?

○ Yes

○ No

12. If yes, would you continue with the selling of these species?

○ Yes

○ No

13. Do you think the trade in exotic small mammals should be regulated by the National Environmental Management: Biodiversity Act?

○ Yes

○ No

14. If yes, how do you think the trade in exotic small mammals should be regulated?

- ☐ Firm regulations
- ☐ Impose fines
- ☐ Other: ______________________

15. If no, why do you think the trade in exotic small mammals should not be regulated?

- ☐ Creates jobs
- ☐ Saves endangered species
- ☐ Forms part of the economy
- ☐ Other: ______________________

16. Do you think the average pet shop loses several small exotic mammals as escapees?

- ○ Yes
- ○ No
- ○ Other: ______________________

17. Do you have any further comments on the sale of small mammals in pet shops?

Your answer ______________________

Submit

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Supplementary Table S3.2 A descriptive statistic on the survey questionnaire of pet shop owners in South Africa from September 2018 to September 2019.

Questions	Number of respondents (*n*)	% respondents	Kruskal-Wallis test by ranks			95% CI
			Chi-square (χ^2)	Degree of freedom	P-value	
Please indicate your Province?	**107**					
Limpopo	5	4.7%				
Gauteng	38	35.5%				
Western Cape	17	15.9%				
Eastern Cape	7	6.5%				
Free State	7	6.5%				
Mpumalanga	3	2.8%				
North West	7	7.5%				
KwaZulu-Natal	20	18.7%				
Northern Cape	3	2.8%				
Which non-native animals do you sell in your pet shop?	**386**		**26.77**	**6**	**8.43e-05****	**1-17.5**
Mammals	87	22.5%				
Reptiles	67	17.3%				
Fish	97	25.1%				
Birds	103	26.6%				
Amphibians	15	3.8%				
Arthropods	10	2.9%				
Molluscs	2	0.5%				
Other	5	1.3%				
Which of these small mammal pets do you sell?	**468**		**42.60**	**13**	**1.52e-05****	**0.5-12.5**
Short-tailed chinchilla (*Chinchilla chinchilla*)	11	2.4%				

Questions	**Number of respondents (*n*)**	**% respondents**	**Kruskal-Wallis test by ranks**			**95% CI**
			Chi-square (χ^2)	**Degree of freedom**	**P-value**	
Long-tailed chinchilla (*Chinchilla lanigera*)	26	5.5%				
Common marmoset (*Callithrix jacchus*)	4	0.9%				
Common degu (*Octodon degus*)	27	5.8%				
Domesticated ferret (*Mustela putorius furo*)	5	1.1%				
Mongolian gerbil (*Meriones unguiculatus*)	22	4.7%				
Guanea pig (*Cavia porcellus*)	63	13.5%				
Golden hamster (*Mesocricetus auratus*)	38	8.1%				
Winter white dwarf (*Phodopus sungorus*)	13	2.8%				
Four-toed hedgehog (*Atelerix albiventris*)	17	3.6%				
House mouse (*Mus musculus*)	65	13.9%				
European rabbit (*Oryctolagus cuniculus*)	76	16.2%				
Norwegian rat (*Rattus norvegicus*)	72	15.4%				
Eastern grey squirrel (*Sciurus carolinensis*)	5	1.1%				
Sugar glider (*Petaurus breviceps*)	11	2.4%				

Questions	**Number of respondents (*n*)**	**% respondents**	**Kruskal-Wallis test by ranks**			**95% CI**
			Chi-square (χ^2)	**Degree of freedom**	**P-value**	
lesser hedgehog tenrec (*Echinops telfairi*)	13	2.8%				
Where do you get your small mammals to sell in your pet shop?	**197**		**17.58**	**6**	**0.001****	**1-11.5**
Pet shop	27	13.7%				
Breeder	67	34.0%				
Online	24	12.2%				
Overseas	25	12.7%				
Wild	3	1.5%				
Rescue	31	15.7%				
Self-bred	20	10.2%				
Has there been an increase in the selling of your small mammal pets?	**87**		**2.53**	**1**	**0.11**	**4-10.5**
Yes	33	34.0%				
No	54	62.1%				
Why do you think the sale is increasing?	**53**		**10.75**	**3**	**0.01***	**0.5-4**
High demand	32	60.4%				
Affordable prices	17	32.1%				
Easier to maintain	3	5.7%				
Other	1	1.9%				
If no. what do you think could be causing the decrease on the sale?	**66**		**28.47**	**4**	**5.30e-07****	**0-8.5**
National Environmental Management: Biodiversity Act (NEM: BA)	35	53.0%				

Questions	Number of respondents (*n*)	% respondents	Kruskal-Wallis test by ranks			95% CI
			Chi-square (χ^2)	Degree of freedom	P-value	
Competition with other pet shops	27	40.9%				
Diseases	2	3.0%				
Species are expensive	0	0.0%				
Other	2	3.0%				
Do you know about the National Environmental Management: Biodiversity Act No. 10 of 2004?	**87**		**14.31**	**1**	**0.02***	**4-11**
Yes	59	67.8%				
No	28	32.2%				
Are the small mammals sold a small percentage of your sales?	**87**		**0.12**	**1**	**0.72**	**7-8**
Yes	43	49.4%				
No	44	50.6%				
If yes. would you continue with the selling of these species?	**46**		**10.96**	**1**	**0.00****	**0.5-7**
Yes	41	89.1%				
No	5	10.9%				
Do you think the trade in exotic small mammals should be regulated by the National Environmental Management: Biodiversity Act?	**87**		**12.30**	**1**	**0.01***	**5-8**
Yes	25	28.7%				
No	62	71.3%				
If yes. how do you think the trade in exotic small mammals should be regulated?	**36**		**7.12**	**3**	**0.03***	**0-3**
Firm regulations	15	41.7%				

Questions	Number of respondents (*n*)	% respondents	Kruskal-Wallis test by ranks			95% CI
			Chi-square (χ^2)	Degree of freedom	P-value	
Impose fines	14	38.9%				
Arrest illegal traders	2	5.6%				
Other	5	13.9%				
If no. why do you think the trade in exotic small mammals should not be regulated?	**122**		**10.48**	**3**	**0.01***	**1.5-6**
Creates jobs	38	31.1%				
Saves engendered species	43	35.2%				
Forms part of the economy	34	27.9%				
Education	7	5.7%				
Do you think the average pet shop loses several sell exotic mammals as escapees?	**87**		**0.70**	**1**	**0.39**	**6.5-8**
Yes	50	57.5%				
No	37	42.5%				

** Represent level of significance below 0.01, while * represent level of significance below 0.05

Supplementary Table S3.2 continue. A descriptive statistic on the survey questionnaire of pet shop owners in South Africa from September 2018 to September 2019.

Please indicate the number of pet shops you think you have in your province?	Pet shops range	No. of respondents (*n*)	% respondents per pet shop range	% respondents per province
Limpopo Province	1-10	5	100%	5 (4.7%)
Gauteng Province	10-20	3	7.9%	38 (35.5%)
	20-30	6	15.8%	
	30-40	5	13.2%	
	40-50	8	21.0%	
	50-80	16	42.1%	
Western Cape	1-10	2	11.8%	17 (15.9%)
	10-20	2	11.8%	
	20-30	3	17.6%	
	30-40	10	58.8%	
Eastern Cape	1-10	7	100%	7 (6.5%)
Free State	1-10	7	100%	7 (6.5%)
Mpumalanga	1-10	3	100%	3 (2.8%)
North West	1-10	7	100%	8 (7.5%)
KwaZulu-Natal	1-10	3	15.0%	20 (18.7%)
	10-20	5	25.0%	
	20-30	12	60.0%	
Northern Cape	1-10	3	100%	3 (2.8%)

CHAPTER 4

Assessing the potential impacts of non-native small mammals in the South African pet trade

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4.1 Abstract

The pet trade is one of the most important pathways by which small mammals are introduced to non-native areas. To prevent the introduction and invasion of non-native pets, an impact assessment protocol is useful in understanding which pets might have potential negative impacts should they escape or be released from captivity. In this study, we used the Generic Impact Scoring System (GISS) to assess the potential effects associated with 24 non-native small mammal species sold in the South African pet trade. European rabbits *Oryctolagus cuniculus*, house mice *Mus musculus*, Norwegian rats *Rattus norvegicus* and eastern grey squirrels *Sciurus carolinensis* had the highest potential impacts for both socio-economic and environmental categories. We found no statistically significant difference between the overall environmental and socio-economic impact scores. Impacts on agricultural and animal production (livestock) were the main mechanisms in the socio-economic category, while the impacts on animals (predation), competition and hybridisation prevailed for environmental impacts. The non-native mammal pet species with high impacts should be strictly regulated to prevent the potential impacts and establishment of feral populations in South Africa.

Keywords GISS, introduction pathways, invasions, impact assessment, policy implementation

4.2 Introduction

Different invasion pathways have been associated with the introduction and spread of non-native species (McNeely 2006; Hulme 2009). These pathways include accidental introductions (e.g. hitch-hikers or contaminants of transported goods) and intentional introductions through horticulture, biocontrol and pet trade (Padilla and Williams 2004; Hulme 2009; Keller et al. 2011). The latter has gained considerable attention over the past decades as the global trade in live animals increases (Keller and Lodge 2007; Faulkner et al. 2016; Ng et al. 2016; Lockwood et al. 2019). Some of the non-native pet species may establish self-sustaining populations through accidental escapes and intentional releases (Gaertner et al. 2015; da Rosa et al. 2017); for example, European rabbit *Oryctolagus cuniculus*, eastern grey squirrel *Sciurus carolinensis*, common marmoset *Callithrix jacchus* and the black tufted-ear marmoset *Callithrix penicillata* (Huynh et al. 2010; da Rosa et al. 2017; Measey et al. 2020).

Non-native pets have been associated with negative impacts on biodiversity, human health, the economy, and agriculture (Marbuah et al. 2014; Su et al. 2015; Shivambu et al. 2020). In Brazil, the common marmoset *C. jacchus* has been reported to negatively affect the population of vulnerable buffy-tufted marmosets *C. aurita* through hybridisation (Nogueira et al. 2011; Malukiewicz et al. 2014). An increase in the trade of non-native small mammal species is also associated with outbreaks of zoonotic diseases, e.g. Salmonellosis in 28 patients in the USA has been linked to pet rodents such as mice, rats and hamsters (Hargreaves 2007). The common marmoset has been implicated in transmitting rabies to humans in Brazil (Kotait et al. 2019). Economic impacts have also been reported for some non-native small mammals, e.g. the European rabbit *O. cuniculus* has been indicated to compete with livestock for pasture in Australia (Fleming et al. 2002). In addition, species such as the eastern grey squirrel, the Norwegian rat *Rattus norvegicus* and the house mouse *Mus musculus* have been reported to cause impacts on infrastructures and crops of economic importance (Signorile and Evans 2007; Almeida et al. 2013; Panti-May et al. 2017).

The negative impacts associated with any introduced species can be partly prevented by prohibiting the trade of those non-native species with known harmful impacts and invasive potential (Vaes-Petignat and Nentwig 2014; van der Veer and Nentwig 2015; da Rosa et al. 2018). In cases where non-native pet species have already been introduced but not yet established, possible impacts can be avoided by preventing their release or escape from captivity (da Rosa et al. 2018). In South Africa, the pet trade has been cited as an invasion pathway for different non-native animals through releases and accidental escapees, including species such as the mallard duck *Anas platyrhynchos* (Gaertner et al. 2015), the rose-ringed parakeet *Psittacula krameri* (Hart and Downs 2014), and the Australian red claw crayfish *Cherax quadricarinatus* (Nunes et al. 2017). The South African National Environmental Management: Biodiversity Act (No. 10 of 2004) (NEM: BA) requires that impact and risk assessments are undertaken by either the issuing authority or the importer before issuing permits for non-native species being imported, sold, kept in captivity or released into the wild (van Wilgen et al. 2008)

Impact and risk assessment protocols are considered to be cost-effective and reliable methods that can be used to identify potential invasion impacts, enable ranking of species and support decision-making (Jeschke et al. 2014; da Rosa et al. 2018; Shivambu et al. 2020). Both impact and risk assessment protocols have been successfully used for fishes (van der Veer and Nentwig 2015), plants (Novoa et al. 2016) and for species in the pet trade (Bomford et al. 2005; Patoka et al. 2014; da Rosa et al. 2018; Weiperth et al. 2018) to investigate the potential invasion risks and impacts.

The present study focused on non-native small mammals sold as pets in South Africa. These non-native small mammal species include rodents, lagomorphs, primates, Eulipotyphla, carnivores, Afrosoricida, and Diprotodontia (Suppl. material 1, Table S4.1). These small mammal pets are traded on different platforms, including online, among breeders and in pet shops (Maligana et al. 2020). There is a relative paucity of information on the potential impacts associated with non-native small mammals sold as pets in South Africa. Non-native small mammal pets such as the sugar glider *Petaurus breviceps* (Heinsohn et al. 2015), the domesticated ferret *Mustela putorius furo* (Davison et al. 1999), the European rabbit (Fleming et al. 2002), the common and the black tufted-ear marmoset (Malukiewicz et al. 2014; Kotait et al. 2019) have been reported to cause impacts in their invaded areas. The aim of the present study was, therefore, to identify which non-native small mammal species sold as pets in South Africa have potentially high environmental and/or socio-economic impacts. We also investigated which impact mechanisms are associated with them. Given that previous studies found that non-native birds and mammals are associated with economic impacts (Kumschick and Nentwig 2010; Nentwig et al. 2010), we predicted that most of the non-native small mammal species traded as pets in South Africa would be more associated with socio-economic impacts rather than environmental impacts. In addition, some of the small mammal species, especially rodents, are associated with human habitation (Garba et al. 2014; Panti-May et al. 2017); therefore, we expected them to cause more economic than environmental impacts.

4.3 Methods

4.3.1 Study species

In this study, pet shops were visited in South Africa to document the list of non-native small mammals sold. The list was complemented with data collated from the online trade. All pet shops and online websites were surveyed four times, once per season (spring, summer, autumn, and winter) between September 2018 and September 2019. During each visit, the numbers of each mammal species were recorded to determine the prevalence. We averaged the numbers of each species for both online and pet shop trade to indicate the most prevalent species. We carried out the impact assessments for 24 non-native small mammals sold in pet shops and online (Maligana et al. 2020; Suppl. material 1, Table S4.1).

4.3.2 Impact assessments

We conducted impact assessments using the Generic Impact Scoring System (GISS) (Nentwig et al. 2010). This tool depends on published evidence associated with environmental and socio-economic impacts of the studied species and allows comparisons and prioritisation. The environmental impacts (Kumschick and Nentwig 2010) were grouped into six impact categories, which included impacts on plants or vegetation (herbivory), impacts on animals (predation), competition, disease transmission, hybridisation, and impacts on ecosystems. The socio-economic impacts were also grouped into six categories, which included impacts on agricultural production, animal production (livestock), forestry production, human infrastructure, human health, and human social impacts (Kumschick and Nentwig 2010; Nentwig et al. 2010). The impact mechanism for each category under environmental and socio-economic impacts ranged from 0 to 5 (0: no impact or literature associated with scored species, 1–2: minor impacts, 3: medium impacts, and 4–5: major impacts) (Nentwig et al. 2010). The potential maximum scores for both environmental and socio-economic impacts is 60. Information on the impacts of the assessed species was retrieved by searching on Google Scholar and Web of Science (https://clarivate.com/) using the scientific and common names of the species in combination with each impact mechanism, for example, "*Oryctolagus cuniculus* impacts on plants or vegetation", "*Callithrix jacchus* impacts on animals", "house mouse impacts on agricultural production", and "*Cebus capucinus* impacts on human social life". In the present study, we only assessed the impacts associated with feral populations of non-native small mammals. We did not assess the reported impacts associated with non-native small mammals in captivity. The assessments of the impacts were based on the publication records entirely from areas outside South Africa.

4.3.3 Statistical analyses

We tested the similarity between the sum of the GISS environmental and socio-economic impact scores using the paired Wilcoxon's signed-rank tests. We tested for significant differences between the mechanisms for environmental and socio-economic impacts using a Kruskal-Wallis test, and the Mann-Whitney pairwise tests were used to test for differences within the species and within the impact mechanisms. All statistical analyses were performed in R statistical software (version 3.4.4, R Core Team, 2018).

4.4 Results

4.4.1 Impact assessments

We found a total of 122 pet shops and seven online websites selling 24 non-native small mammals in South Africa. The European rabbit, the Norwegian rat, the house mouse and the Guinea pig were the most prevalent species in both pet shops and online (Suppl. material 2, Table S4.2). The first three species and the eastern grey squirrel are established species in South Africa (Table 4.1). A total of 106 publications were found and used to rank the impacts of these species. Of the 24 non-native mammal species traded, we could only find published impacts for 10 species and therefore assessed those. The literature ranged between 1 to 23 publications for a single species, and for some of the species, the literature was identical (Suppl. material 2, Table S4.2). The total GISS scores ranged from 3 to 40, with environmental impact ranging from 0 to 18 and socio-economic impacts ranging from 0 to 22 (Table 4.1). The total score for environmental impact was 115 and for socioeconomic impact was 81 (Table 4.1). When comparing the overall scores between the two impacts, there was no significant difference between overall environmental and socio-economic impact scores (Wilcoxon signed-rank test, $V = 23$, $P = 0.1022$). The European rabbit, Norwegian rat and house mouse had the highest overall GISS scores (between 32 and 40), representing between 53% and 67% of the maximum impact assessment score (i.e. 60) (Table 4.1).

All the non-native mammal species assessed in the present study had environmental impacts, except for the Mongolian gerbil *Meriones unguiculatus* (Table 4.1, Fig. 4.1a). There was no significant difference between the potential environmental impacts of the non-native small mammal species assessed (Kruskal-Wallis test; $\chi^2 = 3.01$, df = 9, $P = 0.90$). The species with the highest environmental impact were the European rabbit, followed by the house mouse and the Norwegian rat (Table 4.1). These species represented between 50% and 60% of the maximum environmental impact score (i.e. 30).

Seven out of 10 of the non-native mammal species traded as pets had socio-economic impacts in the present study (Table 4.1, Fig. 4.1b). There was a significant difference between the socio-economic impact scores for the 10 non-native small mammals traded as pets (Kruskal-Wallis test, $\chi^2 = 22.27$, df = 9, $P = 0.003$, Fig. 4.1b). The European rabbit, the house mouse, and the Norwegian rat had significantly higher socioeconomic impacts when compared with the other seven species (Mann-Whitney pairwise test, Bonferroni corrected p values, $P < 0.001$, Table 4.1, Fig. 4.1b). They represented more than 50% of the maximum socio-economic impact score (i.e. 30).

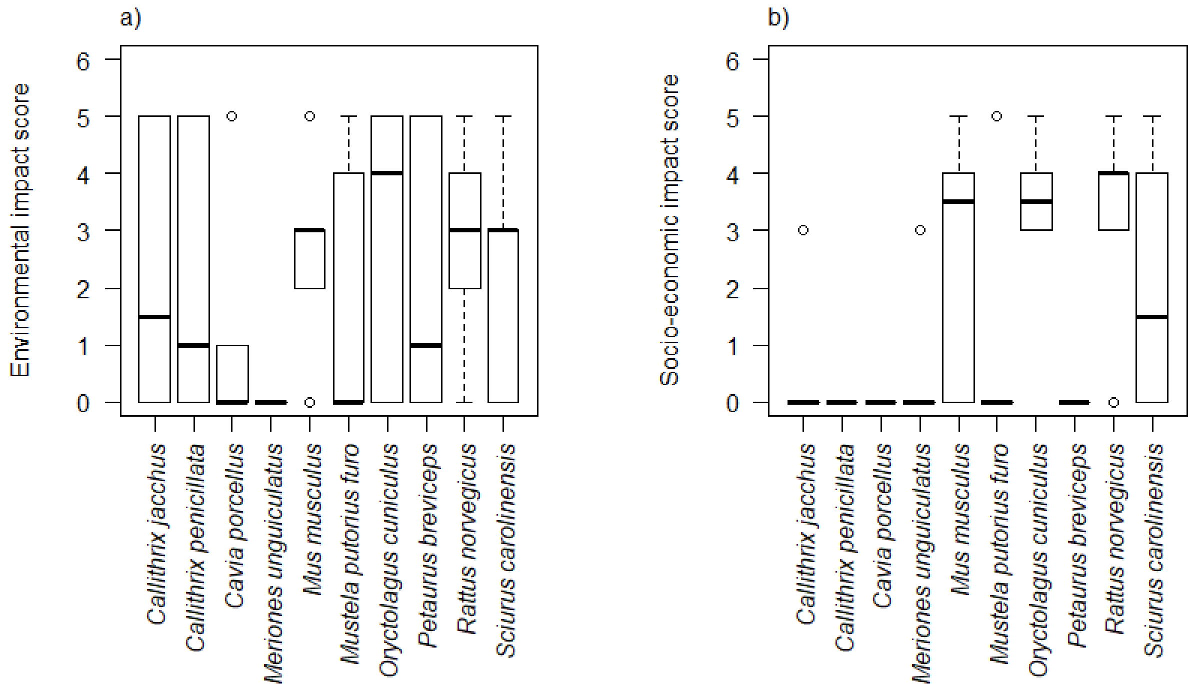

Fig. 4.1 Box-plot showing a) environmental and b) socio-economic impact scores for the10 non-native small mammals available in the South African pet trade. (Boxes shows the 25th and 75th percentiles and whiskers (values below and above 5 and 4.5 for environmental and socio-economic respectively were considered as outliers) indicate the maximum range, interquartile range, median, and the minimum range).

4.4.2 Environmental impacts mechanisms

Between the environmental impact mechanisms, significant differences were found (Kruskal-Wallis test, $\chi^2 = 15.63$, df = 5, $P = 0.002$, Table 4.1). The only significant difference found was between the impact on animals (predation), disease transmission and the impact on the ecosystem (Mann-Whitney pairwise test, Bonferroni corrected p values, $P < 0.001$). The impact on animals (predation), competition, and hybridisation were the most common mechanisms, followed by the impact on plants and vegetation (herbivory), impact on ecosystems, and disease transmission (Table 4.1). For each impact mechanism, different species had maximum scores, i.e., plants and vegetation (herbivory) (eastern grey squirrel), animals (predation) (Guinea pig, house mouse, domesticated ferret, the European rabbit, sugar glider and Norwegian rat), competition (common marmoset, black tufted-ear marmoset, European rabbit and sugar glider) and hybridisation (common marmoset and black tufted-ear marmoset) (Table 4.1).

Table 4.1. The GISS scores of 10 non-native small mammal species sold in the South African pet trade. The sum of each impact category is given, and the total impact indicates the overall sum of environmental and socio-economic impacts for each species. Detailed scores for each species and literature used are available in Supplementary Material 2, Table S4.2. An asterisk indicates species established in South Africa (see Picker and Griffiths 2017, and Measey et al. 2020).

		Environmental impacts							Socio-economic impact								
Species	**Common names**	**Plants or vegetation (Herbivory)**	**Animals (Predation)**	**Competition**	**Diseases transmission**	**Hybridisation**	**Ecosystems**	**Overall environmental scores**	**Agricultural production**	**Animal production (Livestock)**	**Forestry production**	**Human**	**Human health**	**Human social life**	**Overall socio-economic impacts**	**Overall GISS impact scores**	**Number of literature used**
Callithrix jacchus	Common marmoset	0	3	5	0	5	0	**13**	0	0	0	0	3	0	**3**	**16**	10
Callithrix penicillata	Black tufted ear marmoset	0	2	5	0	5	0	**12**	0	0	0	0	0	0	**0**	**12**	8
Cavia porcellus	Guinea pig	0	5	0	0	1	0	**6**	0	0	0	0	0	0	**0**	**6**	2
Meriones unguiculatus	Mongolian gerbil	0	0	0	0	0	0	**0**	3	0	0	0	0	0	**3**	**3**	2
*Mus musculus**	House mouse	3	5	2	0	3	3	**16**	5	4	0	4	3	0	**16**	**32**	23
Mustela putorius furo	Domesticated ferret	0	5	0	0	4	0	**9**	0	5	0	0	0	0	**5**	**14**	9
*Oryctolagus cuniculus**	European rabbit	4	5	5	0	0	4	**18**	5	4	4	3	3	3	**22**	**40**	23
Petaurus breviceps	Sugar glider	0	5	5	0	2	0	**12**	0	0	0	0	0	0	**0**	**12**	7
*Rattus norvegicus**	Norwegian rat	3	5	3	0	0	4	**15**	4	4	0	5	4	3	**20**	**35**	20

		Environmental impacts							Socio-economic impact								
Species	**Common names**	**Plants or vegetation (Herbivory)**	**Animals (Predation)**	**Competition**	**Diseases transmission**	**Hybridisation**	**Ecosystems**	**Overall environmental scores**	**Agricultural production**	**Animal production (Livestock)**	**Forestry production**	**Human**	**Human health**	**Human social life**	**Overall socio-economic impacts**	**Overall GISS impact scores**	**Number of literature used**
*Sciurus carolinensis**	Eastern grey squirrel	5	3	3	3	0	0	**14**	4	0	5	3	0	0	**12**	**26**	10
Overall scores	15	38	28	3	20	11	**115**	21	17	9	15	13	6	**81**	**196**	10	

4.4.3 Socio-economic impacts mechanisms

All assessed non-native small mammal species (n = 10) had socio-economic impacts except for the black tufted-ear marmoset, the Guinea pig and the sugar glider (Table 4.1). No significant differences between the impact mechanisms were found (Kruskal-Wallis test, χ^2 = 2.89, df = 5, P = 0.54, Table 4.1). However, the most often mentioned impact mechanism was on agricultural production with a summed score of 21 (Table 4.1). Different species had maximum scores for each impact mechanism, namely, agricultural production (house mouse and European rabbit), animal production (livestock) (domesticated ferret), forest production (eastern grey squirrel) and human infrastructure (Norwegian rat) (Table 4.1). Four out of 10 species had impacts on human health, and the Norwegian rat had the highest impact (Table 4.1). Only the European rabbit and the Norwegian rat had an impact on human social life, and these species had similar impact scores (Table 4.1).

4.5 Discussion

The non-native small mammals traded as pets and assessed in the present study had no significant differences between the overall environmental and socio-economic impact categories. However, a related study on feral mammal species by Hagen and Kumschick (2018) found a difference between environmental and socio-economic impacts where environmental impacts were significantly higher when compared with socio-economic impacts. An explanation for this difference could be that different domesticated non-native species were scored, and only three species were identical between the studies (Hagen and Kumschick 2018). Three species, the European rabbit, Norwegian rat, and house mouse, were estimated to have the highest overall impact in this study. Previous studies have also shown that these species have relatively high impacts in both environmental and socio-economic impact categories (Nentwig et al. 2010; Hagen and Kumschick 2018).

The environmental impacts of these three species with high scores were related to their impacts on other animals (predation) and competition because they have caused the extinction of native species or generally compete with several species of high conservation concern. For example, the extinction of the Laysan crake *Porzana palmeri* in Hawaii has been linked to the introduction of Guinea pigs and European rabbits, and in Australia, rabbits outcompete the vulnerable rufous hare-wallaby *Lagorchestes hirsutus* for food and space (Lees and Bell 2008; Hume 2017). The house mouse and the Norwegian rat are associated with the reduction of native species and are also responsible for the extinction of several bird, insect and reptile species on different islands (Atkinson 1985; Marris 2000; Cuthbert and Hilton 2004; Zeppelini et al. 2007; Jones et al. 2008; Dagleish et al. 2017). These three species represent the most popular species in the South African pet trade industry (Maligana et al. 2020; Suppl. material 1, Table S4.1). In addition, the European rabbit is regarded as invasive on South African offshore islands, while the Norwegian rat and the house mouse are invasive on the mainland and offshore islands (Picker and Griffiths 2017; Measey et al. 2020). Consequently, these species may likely have higher potential impacts than other species scored in this study, given their establishment status in South Africa. There is also a lack of studies on the actual environmental and socio-economic impacts of these small mammals recorded in South Africa (Hagen and Kumschick 2018). It is also possible that most of the impacts reported elsewhere for these non-native mammals have already taken place in South Africa but are not yet documented. The results for the present study were different when compared with a study on non-native invertebrate pets in South Africa which found that popular species had minimal impacts (Nelufule et al. 2020). This difference may be explained by the fact that invertebrates are generally not well studied when compared with mammal species (Nentwig et al. 2010; Kumschick et al. 2015; Hagen and Kumschick 2019; Nelufule et al. 2020). Some popular mammal species in the pet trade, such as the sugar glider, have previously been reported to have relatively high potential ecological risk (da Rosa et al. 2018). This species can survive in the wild and has been reported to cause negative impacts on biodiversity by preying on the critically endangered swift parrot *Lathamus discolor* in Tasmania, Australia (Campbell et al. 2018). If this species is released from captivity, it can cause similar impacts in South Africa, as it is also popular in the pet trade, especially in the online trade (Supplementary material Table S4.1).

The common marmoset and the black tufted-ear marmoset were the only species scoring high impacts through hybridisation. These two species have been reported to threaten the vulnerable populations of buffy-tufted marmosets *C. aurita* and Wied's marmosets *C. kuhlii* in Brazil (Nogueira et al. 2011; Cezar et al. 2017; Moraes et al. 2019). The hybrids of these two primates have been reported in the wild, and they are also fertile (Ruiz Miranda et al. 2006; Oliveira and Grelle 2012; Malukiewicz et al. 2014). It is evident that these primates are a threat to populations of other marmosets in their introduced ranges. However, it is unlikely that these species will threaten the populations of other primates in South Africa as there are no native marmoset species. However, this does not suggest that these species will not cause impacts through other mechanisms as there is evidence of impacts on other animals through predation (Alexandrino et al. 2012).

The only species which recorded maximum impact on forestry production and plants or vegetation (herbivory) in the present study was the eastern grey squirrel. This species scored a maximum potential impact because it has been reported to cause impacts to endangered plant species, and its impacts have also resulted in major economic losses. For example, Lawton et al. (2007) reported that economic damage caused by eastern grey squirrels to beech *Fagus sylvatica*, sycamore *Acer pseudoplatanus* and ash *Fraxinus excelsior* (listed as near threatened by IUCN, (Khela 2013)) woodlands in the UK were estimated to be ~£10 million (Williams et al. 2010; Merrick et al. 2016). This species has also been reported to damage *Populus* ×

euroamericana plantations (Signorile and Evans 2007). Given that this species thrives in the urban and commercial areas in South Africa, it is likely to cause impacts on forestry production, nut, fruit and vegetable crops, and also telecommunication cables (Measey et al. 2020).

Several non-native mammal species assessed in the present study are regarded as agricultural pests (Reid et al. 2007; Girling 2013). Therefore, the impact on agriculture was high when compared with other impact mechanisms. The species responsible for the maximum potential impact under this mechanism were the house mouse and the European rabbit. These species scored high because their impacts were mostly associated with major economic losses on agriculture, and also their eradication plans required the application of pesticides which are expensive and have negative impacts (Twigg et al. 2002; Williams et al. 2010; Haniza et al. 2015; Capizzi 2020; Mill et al. 2020). In developing countries, invasive rats and mice compete with humans for food (Stenseth et al. 2003), targeting various crops such as cereals, rice, palm oil, fruits, cocoa, and sugarcane, which results in a significant economic loss and affects food security (Tobin and Fall 2004; Varnham 2006). The United Nations reported that in 1982 rats and mice damaged ~42 million tons of food globally, worth ~US $30 billion worldwide (Almeida et al. 2013). Although there is a lack of information on the impacts associated with non-native invasive rats and mice in South Africa, these species are likely to be causing socio-economic impacts. Studies in South Africa indicated that pesticides are used to control rats and mice in different households in urban areas (Balme et al. 2010; Rother 2012; Roomaney et al. 2012). This may suggest that these rodents may be problematic, but little attention has been given to the economic losses associated with control measures and other socio-economic impacts in general.

Domesticated ferrets were responsible for the highest impact through the animal production (livestock) mechanism. In New Zealand, they have been reported to host the *Bovine tuberculosis* disease that has been transmitted to livestock and threatens production of beef, dairy and venison markets (Ragg et al. 1995; Byrom 2002; de Lisle et al. 2008). Domesticated ferrets might also pose the risk of transmitting *B. tuberculosis* in South Africa, given that they are kept as pets and have become invasive after accidental escapes in New Zealand (Byrom 2002). The Norwegian rat had the highest score for infrastructural impact. Their damage to infrastructure includes gnawing of electric cables, burrowing, and contaminating water and food through droppings and urine (Johnson 2008; Garba et al. 2014; Panti-May et al. 2017). Their gnawing on communication cable and wires has further resulted in fires; as a result, repellents/rodenticides are generally used to control them (Shumake et al. 2000). The Norwegian rat also had a high potential impact on human health in the present study because they carry pathogens that are transmittable and fatal to humans, such as *Bartonella*, *Echinococcosis* and *Seoul* virus (Firth et al. 2014; Abdel-Moein and Hamza 2016). This rat has also been reported to bite humans, causing wounds that require medical attention (Donoso et al. 2004; Garba et al. 2014; Panti-May et al. 2017). It is possible that non-native invasive rats may threaten the health of humans in South Africa, given their wide distribution in the urban landscapes and having been found to carry zoonotic agents such as helminths, toxoplasmosis and leptospirosis (Taylor et al. 2008; Julius et al. 2018).

Only the European rabbit and the Norwegian rat had an impact on human social life, and these species had the same impact scores. Rabbit burrows cause damage to gardens and golf courses (Brown 2012). Norwegian rats also make damaging burrows, for example, in cities, especially under concrete sidewalks and in backyards (Sullivan 2004; van Adrichem et al. 2013). In South Africa, the Norwegian rat would likely cause severe human social life impacts when compared with the European rabbit, given that it is distributed in urban areas and rabbits are present on the offshore islands only (Bastos et al. 2011; Julius et al. 2018; Measey et al. 2020). However, impacts associated with the European rabbit may be severe on the offshore islands where the species is known to reduce vegetation (Sherley 2016). Should species with high impacts be released or escape from captivity and establish feral populations, impacts reported in the present study may occur and results in the reduction of biodiversity and economic loss during eradication and the repairing of damages caused.

4.6 Conclusions and recommendations

The present study showed that several of the South African non-native small mammal pets that are traded and were assessed pose either potentially high environmental and/ or socio-economic impacts as documented in other countries. But of great concern are the following species: the European rabbit, the house mouse, the Norwegian rat and the eastern grey squirrel which have been reported as established in South Africa and its offshore islands (Picker and Griffiths 2017; Measey et al. 2020). The establishment of the European rabbit and the eastern grey squirrel in South Africa is associated with escapees from captivity (Measey et al. 2020). It is likely that these species are causing similar impacts in South Africa but unreported. We recommend that established species with high impacts should be prioritised for eradication and management. The trade for those species with significantly higher environmental and socio-economic impacts should be stopped and monitored, prioritised in policy development and regulations implemented so that their potential impacts in South Africa may be prevented. Regulations on the trade of non-native species exist, but these regulations are not implemented in many countries, and furthermore, in South Africa, there is an increased demand for non-native pets and ongoing illegal trade (van Wilgen et al. 2008; Martin et al. 2018; Siriwat and Nijman 2018). To prevent impacts by non-native pet species, countries may need to document alien species traded, and do impact or risk assessments to identify invasive species, which may require management.

4.7 Acknowledgements

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4.9 Supplementary materials

Table S4.1 The mean numbers showing the prevalence of the 24 non-native mammal species sold in the South African pet trade between September 2018 and September 2019. An asterisk (*) indicate species (n = 10) that their impacts were assessed based on data availability

Scientific name	**Common name**	**Species prevalence**	
		Pet shop	**Online**
Atelerix albiventris (Wagner, 1841)	Four-toed hedgehog	812	81
Callithrix jacchus (Linnaeus, 1758) *	Common marmoset	121	40
Callithrix penicillata (É.Geoffroy Saint-Hilaire, 1812) *	Black tufted-ear marmoset	119	37
Cavia porcellus (Linnaeus, 1758) *	Guinea pig	3 192	270
Cebuella pygmaea (Spix, 1823)	Pygmy marmoset	0	6
Cebus capucinus (Linnaeus, 1758)	White-faced capuchin	0	5
Chinchilla chinchilla (Lichtenstein, 1829)	Short-tailed chinchilla	416	40
Chinchilla lanigera (Molina, 1782)	Long-tailed chinchilla	400	81
Echinops telfairi (Martin, 1838)	Lesser hedgehog tenrec	117	8
Meriones unguiculatus (Milne-Edwards, 1867) *	Mongolian gerbil	213	8
Mesocricetus auratus (Waterhouse, 1839)	Golden hamster	1 195	81
Mus musculus (Linnaeus, 1758) *	House mouse	1 368	125
Mustela putorius furo (Linnaeus, 1758) *	Domesticate ferret	52	41
Octodon degus (Molina, 1782)	Common degu	385	60
Oryctolagus cuniculus (Linnaeus, 1758) *	European rabbit	6 170	1 195
Petaurus breviceps (Waterhouse, 1838) *	Sugar glider	75	132
Phodopus sungorus (Pallas, 1773)	Winter white dwarf hamster	2 052	155
Potos flavus (Schreber, 1774)	Kinkajou	0	39
Rattus norvegicus (Berkenhout, 1769) *	Norwegian rat	3 195	262
Saguinus midas (Linnaeus, 1758)	Red-handed tamarin	0	8
Saguinus oedipus (Linnaeus, 1758)	Cotton-top tamarin	0	5
Saimiri sciureus (Linnaeus, 1758)	Common squirrel monkey	0	14
Sciurus carolinensis (Gmelin, 1788) *	Eastern grey squirrel	0	6

Scientific name	Common name	Species prevalence	
		Pet shop	Online
Vulpes zerda (Zimmermann, 1780)	Fennec fox	0	32

Table S4.2 Detailed assessment of non-native mammalian species sold in the pet trade in South Africa.

This dataset is made available at: https://doi.org/10.3897/neobiota.60.52871.suppl2

CHAPTER 5

Predicting the potential distribution of non-native small mammalian species sold in the South African pet trade

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5.1 Abstract

The pet trade is one of the main pathways of the introduction of several small mammals worldwide. In South Africa, non-native small mammals are traded as pets, and so far, only four of these species are considered invasive. We surveyed 122 pet stores and seven websites to determine the non-native small mammals traded in South Africa between September 2018 to 2019. We found a total of 24 small mammal species sold and selected them for analysis based on their popularity on trade, invasion histories and potential economic and socio-economic impacts. Distribution records were used to estimate their potential distribution using species distribution modelling (SDM) based on ecological niches. Of the recorded species, 14 were selected based on the selection criterion. Results showed that commonly available species with invasion histories elsewhere and South Africa had the largest predicted distributions. These included the European rabbit (*Oryctolagus cuniculus*), the house mouse (*Mus musculus*) and the Norwegian rat (*Rattus norvegicus*). As the latter is known to be synanthropic, the human footprint was found to explain its potential suitability. We considered seven species as potential invaders given their invasion history, invasion pathway, availability in the pet trade, and larger potential distributions. To prevent invasions and impacts associated with these species, we recommend monitoring their trade and surveillance, especially in highly suitable areas within or close to their selling points.

Keywords: Human footprint, species distribution modelling, invasive species, introduction pathway, impact

5.2 Introduction

Several mammalian species have been introduced around the world for different purposes, including pest control, research, food, fur markets, game, hunting, zoo, and as pets (Long, 2003; Parkes & Murphy, 2003; Borroto-Páez, 2009; Patoka et al., 2018; Measey et al., 2020). Mammalian species are among the most successful invaders worldwide than other vertebrate taxa (Clout & Russell, 2007; Jeschke, 2008; Latham et al., 2017). Mammalian species' success as biological invaders is mostly linked to their ability to breed successfully, extensive physiological tolerance, association with humans, broad habitats, and diets (Long, 2003; Clout & Russell, 2007; Latham et al., 2017). Invasive mammalian species have been associated with negative impacts on agriculture, human health, infrastructure, native fauna and biota in general (Iriarte et al., 2005; Pavlin et al., 2009; Bertolino et al., 2014; Latham et al., 2017; Shivambu et al., 2020a).

It is vital to investigate the invasion history and potential distribution of non-native species to prevent them from becoming invasive and potentially cause impacts. Studies have suggested that matching the climate between the native and non-native areas of a species is essential in identifying the invasion potential for that species (Bomford, 2009; Filz et al., 2018). The species distributing modelling (SDM) is a widely used tool to predict potentially suitable areas where non-native species may establish and become invasive if introduced into favourable environments (Thomaes et al., 2008; Stevenson-Holt et al., 2014; Ramírez-Albores et al., 2016).

The SDM is also known as a bioclimatic envelope, ecological niche modelling or habitat suitability modelling, which uses an organism's occurrence records combined with geographical environmental variables to predict species suitability (Guisan & Zimmermann, 2000; Elith et al., 2006; Peterson et al., 2011; Booth et al., 2014; Runquist et al., 2019). The SDM has been applied in a range of fields, including biodiversity conservation and wildlife management (Rodríguez et al., 2007; Araújo & Peterson, 2012; Booth et al., 2014), climate change (Beaumont et al., 2008), species extinction assessment (Thomas et al., 2004), and risk assessment (Jiménez-Valverde et al., 2011; Uderbayev et al., 2017; Jarnevich et al., 2018; Ramírez-Ortiz et al., 2020). Distribution modelling can also be used to develop and implement early detection, warnings and prevent potential invaders (Fletcher et al., 2016; Steen et al., 2019). Some studies have suggested that invasive species in some parts of the world are likely to become invasive in other regions, given that these areas have similar environmental suitability (Kolar et al., 2001; Bomford et al., 2009). Additionally, socio-economic factors such as human population density, cropland, built environments, pasture land, railways, night-time lights, roads, and manoeuvrable waterways have been responsible for the invasion of several species (Sanderson et al., 2002; Pyšek et al., 2010; Gallardo et al., 2015). For example, the invasion success of the commensal rodents such as the house mouse (*Mus musculus* (Linnaeus, 1758)) and the Norwegian rat (*Rattus norvegicus* (Berkenhout, 1769)) (Schwarz & Schwarz, 1943; Panti-May et al., 2016; Phifer-Rixey & Nachman, 2015; Schweinfurth, 2020).

Several non-native small mammalian species introduced through the pet trade have established feral populations outside their native ranges, e.g. the sugar glider (*Petaurus breviceps* (Waterhouse, 1838)) and the Common marmoset (*Callithrix jacchus* (Linnaeus, 1758)) (Iriarte et al., 2005; da Rosa et al., 2017). The sale of non-native small mammals typically remains unregulated, leading to many species translocated between the regions, sometimes resulting in pet releases or escapes (Richardson et al., 2003; Bush et al., 2014). Several non-native small mammals, including the world worst invasive species, such as the house mouse and the Norwegian rat, are sold in the South African pet trade (Maligana et al., 2020). Relatively little has been done to investigate if any of these species sold in South Africa have potential climatic suitability. Therefore, we compiled a list of non-native small mammalian species sold online and in physical pet stores in South Africa to determine the following; 1) their availability, 2) invasion history and pathways, and 3) their potential distribution in South Africa. We predicted that species with high availability, history of invasion elsewhere and extensive occurrence records would have greater invasion potential. In addition, we expected the human footprint to influence the potential distribution of the house mouse and the Norwegian rat.

5.3 Methods

5.3.1 Data collection

We obtained information about the trade in non-native small mammalian species in South Africa by monitoring online trade and surveying physical pet stores (See Maligana et al., 2020; and Shivambu et al., 2021). Geographical coordinates were recorded for each pet store and areas where species were advertised on online platforms (Fig. 5.1). We developed the map showing study areas (Fig. 5.1) using ArcGIS (version 10.4.1; ESRI 2018). Pet stores and online trade were surveyed four times, once each season, between September 2018 and September 2019. A total of 122 pet stores from nine South African Provinces which sell live non-native species were visited and excluded all pet product stores. We compiled a list of traded non-native small mammalian species. It included species names (common and scientific) and the number of pet stores where the species were sold (Appendix A5.1). We used the following criteria to evaluate species availability in the pet trade following examples by Chucholl (2013) i) "very rare", species available for a short period in either one source of trade (online or pet store), few Provinces (<4) or online platforms (<3) and in low quantity; (ii) "rare", species occasionally available in either one source of trade, few Provinces or online platforms and in low quantity; (iii) "common", species frequently available in either one source of trade, more Provinces or online platforms and high quantity; and (iv) "very common", species always available in all the sources of trade, more Provinces (>4) or online platforms (>3) and high quantity.

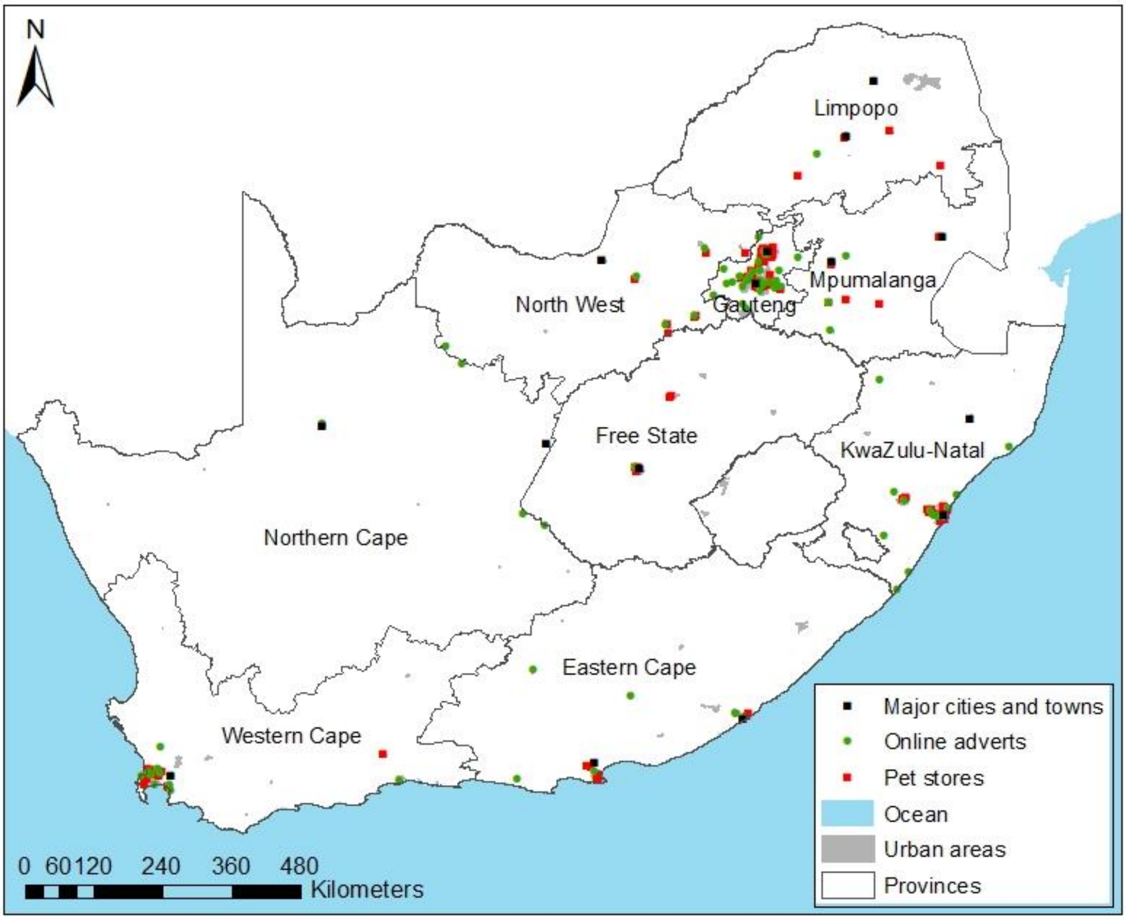

Fig. 5.1 A map showing localities of pet stores, online advertisements and major cities where non-native small mammals were sold as pets in South Africa in the present study between September 2018 and September 2019.

5.3.2 Species occurrence data

We found a total of 24 species for sale, but we excluded ten species based on the following criteria; 1) popular in the South African pet trade (Maligana et al., 2020; Shivambu et al., 2021), 2) distribution records in both or either native and introduced ranges, 3) history of invasion elsewhere, and 4) potential environmental and socio-economic impacts (Shivambu et al., 2020a). To develop species distribution modelling, we compiled occurrence records from the following sources, invasive species compendium (ISC) (http://www.cabi.org/isc/), and Global Biodiversity Information Facility (GBIF; https://www.gbif.org/). The datasets included museum specimens from both or either native or invaded ranges. The distribution records were cleaned by removing records falling into the ocean and duplicates using Biogeo package in R (Robertson et al., 2016). We converted the downloaded datasets to spatial points readable in R (Shivambu et al., 2020b).

5.3.3 Model fitting, prediction and evaluation

We used the species distribution modelling (SDM) package (Naimi & Araújo, 2016) in R (version 3.6.1, R Core Team, 2018) to develop ecological niche models of the 14 non-native small mammalian species traded in South African online and pet stores. A set of 19 bioclimatic variables (https://www.worldclim.org/, Hijmans et al., 2005; Fick & Hijmans, 2017) at 10-min. spatial resolution were downloaded and used as predictors to describe each small mammal species suitability. We tested for correlations between bioclimatic variables using the variance inflation factor function (VIF; Marquardt, 1970) and Pearson (r) correlation coefficients to detect collinearity. The bioclimatic variables that were collinear were excluded when building the model, and nine or ten variables were used for each species (see Appendix A5.2). We further included a global map of human influence "human footprint" (Sanderson et al., 2002) as our additional predictor variable for the house mouse and the Norwegian rat as their spread has been associated with human existence. The human footprint index was downloaded from https://sedac.ciesin.columbia.edu/data/set/wildareas-v3-2009-human-footprint (Venter et al., 2018). The potential distribution for these two rodents was produced using ArcGIS (version 10.4.1; ESRI, 2018).

We fitted the model using Maxent's maximum entropy algorithm (Maxent: Phillips et al., 2006). To project potential species distribution models, Maxent requires presence and pseudo-absences records (Guisan & Zimmerman, 2000; Guisan & Thuiller, 2005; Naimi & Araújo, 2016). For this study, 10 000 pseudo-absences records were randomly drawn from a defined background at average runs of 100 bootstrap replications (Stockwell & Peterson, 2002; Phillips, 2008; Barbet-Massin et al., 2012; Fourcade et al., 2014). The occurrence data for each species were partitioned into training and testing dataset using *k*-fold partitioning. About 80% of the dataset was used as training and the remaining 20% as testing dataset. The convergence threshold was $1\text{x}10^{-5}$ based on 10 replications, and parameters were set to 5000 iterations.

Model performance for species was evaluated using the independent-threshold statistic, AUC (Area Under Curve) of the receiver operating characteristic curve (ROC) (Fielding & Bell, 1997). The AUC values range from 0 to 1, with values below 0.7 considered poor, between 0.7 and 0.9 considered good, and greater than 0.9 considered excellent (Swets, 1988; Fielding & Bell, 1997). Ensembles of all the Maxent methods for each species were generated to create a consensus model among them. The range distribution map for each species was downloaded using R statistical software (version 3.6.1, R Core Team, 2018) for analyses.

5.4 Results

We found a total of 24 non-native small mammals sold in the South African pet trade. Four species, the European rabbit, the Norwegian rat, the house mouse and the Guinea pig (*Cavia porcellus* (Linnaeus, 1758)), were very common in the physical pet stores (Table A5.1). These species were also very common in the online trade, followed by the winter white dwarf hamster (*Phodopus sungorus* (Pallas, 1773)) and the sugar glider (Table A5.1). Nine species, the European rabbit, the Norwegian rat, the house mouse, the eastern grey squirrel (*Sciurus carolinensis* (Gmelin, 1788)), the common marmoset, the black-tufted ear marmoset

(*Callithrix penicillata* (É.Geoffroy Saint-Hilaire, 1812)), the common squirrel monkey (*Saimiri sciureus* (Linnaeus, 1758)), the sugar glider and the domesticated ferret (*Mustela putorius furo* (Linnaeus, 1758)) are listed as invasives in different countries (Table 5.1). The invasion of these species, excluding the house mouse, is typically associated with intentional releases or accidental escapes of captive animals (Table 5.1). Of the recorded species, only 14 met the selection criterion for the species distribution modelling and therefore, their results were presented.

Table 5.1 List of non-native small mammal species sold as pets in South Africa, including their availability in the pet trade (VC, very common; C, common; R, rare; VR, very rare), native ranges, their status in South Africa, invasion history and pathways.

Scientific name	Common name	Availability	Native area	Status in SA	Countries invaded	Invasion pathway	Distribution records and invasion history references
Atelerix albiventris	African pygmy hedgehog	VC	Eastern Africa	Captivity	Not invasive	Not invasive	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.tftrhb
Callithrix jacchus	Common marmoset	R	East-central Brazil	Captivity	Southeast and Northeast Brazil	Release and escape (pet)	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.qrrkfj Rylands et al. (2008) da Rosa et al. (2017)
Callithrix penicillata	Black-tufted ear marmoset	VR	East-central Brazil	Captivity	Southeast Brazil	Release and escape (pet)	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.kgmj7v Rylands and Mendes, 2008 da Rosa et al. (2017)
Cavia porcellus	Guinea pig	VC	South America	Captivity	Not invasive	Not invasive	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.ekshfw
Meriones unguiculatus	Mongolian gerbil	R	Mongolia and north-eastern China	Captivity	Not invasive	Not invasive	GBIF.org (1 February 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.srmaay
Mus musculus	House mouse	VC	Eurasia	Invasive	All continents except Antantica	Accidental escape (hitchhikers on trading ships and cargos)	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.ag7cpj Long (2003)
Mesocricetus auratus	Golden hamster	VC	Syria, Turkey, Greece, Romania and Belgium	Captivity	Not invasive	Not invasive	GBIF.org (1 February 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.q3zyw5
Mustela putorius furo	Domesticated ferret	C	Western Eurasia and North Morocco	Captivity	Azores, United Kingdom and New Zealand	Intentional releases and accidental escape (pet,	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.mrnhzs Buckley et al. (2007)

Scientific name	Common name	Availability	Native area	Status in SA	Countries invaded	Invasion pathway	Distribution records and invasion history references
						hunting, fur farming)	Long (2003) Booy et al. (2015)
Oryctolagus cuniculus	European rabbit	VC	Europe	Invasive	All continents	Intentional release and accidental escape (food or farming)	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.e84j6c Long (2003) Braysher (2017)
Octodon degus	Common degu	C	West-central Chile	Captivity	Not invasive	Not invasive	GBIF.org (3 February 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.qryxn5
Petaurus breviceps	Sugar glider	VC	Australia and New Guinea	Captivity	Tasmania	Accidental escape (pet)	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.rt4yry Gunn (1846) Heinsohn (2004)
Rattus norvegicus	Norwegian rat	VC	China, Russia, Japan	Invasive	All continents except Antantica	Accidental escape (hitchhikers on trading ships and cargos)	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.79f5df Long (2003)
Saimiri sciureus	Common squirrel monkey	VR	South America	Captivity	Rio de Janeiro State	Release (pet)	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.h72pwt Camarotti et al. (2015) da Rosa et al. (2017)
Sciurus carolinensis	Eastern grey squirrel	VR	Eastern North America	Invasive	South Africa, Ireland, Italy, United Kingdom, North America	Intentional release and accidental escape (pet, ornamentation)	GBIF.org (17 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.nz5yca Long (2003) Huynh et al. (2010)

The European rabbit, the Norwegian rat, the house mouse and the eastern grey squirrel are regarded as invasive species in South Africa and its offshore islands. Among these four species, the house mouse had a potentially larger predicted distribution, covering all the South African provinces, followed by the European rabbit, the Norwegian rat and the eastern grey squirrel (Fig. 5.2). The predicted distributions for the European rabbit and the Norwegian rat were, however, on the same areas, covering the large part of the coastal areas of Western Cape, Eastern Cape and KwaZulu-Natal Provinces (Fig. 5.2). The predicted distribution for the eastern grey squirrel was not large and only within the small section of the KwaZulu-Natal and Western Cape coasts (Fig. 5.2). The predicted distribution for these four species was within the areas where the species have been reported to occur (Fig. 5.2). In addition, the current selling points for these species were within the projected distribution, except for only one point in Gauteng Province for the eastern grey squirrel (Fig. 5.2).

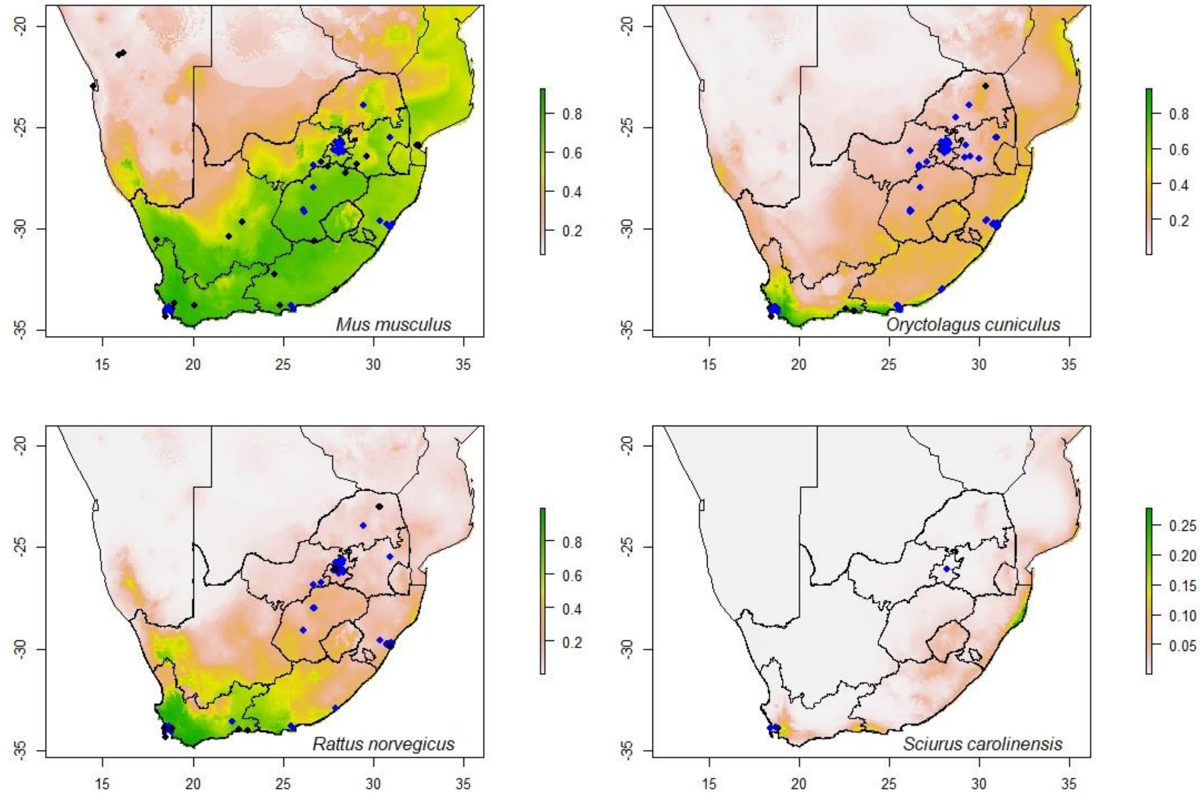

Fig. 5.2 The potential distribution from ecological niche modelling of the four non-native invasive small mammalian species, the house mouse (*Mus musculus*), the European rabbit (*Oryctolagus cuniculus*), the Norwegian rat (*Rattus norvegicus*) and the eastern grey squirrel (*Sciurus carolinensis*) in South Africa (Note: The colour ramp threshold on the right measured the suitability; green indicates the most suitable areas, decreasing to yellow, orange, with light gold and white being unsuitable). Black dots indicate current distribution records, and blue dots indicate selling points.

We found that the model performed well in predicting the potential distribution for all four species, with the AUC value of 0.862 for the house mouse, 0.944 for the European rabbit, 0.97 for the Norwegian rabbit and 0.98 for the eastern grey squirrel (Table A5.2). Bio 3 (Isothermality (Bio2/Bio7) (×100)) and bio 19 (Precipitation of Coldest Quarter) contributed the most to the models for the house mouse and the Norwegian rat. For the European rabbit, bio 19 and bio 4 (Temperature Seasonality (standard deviation ×100)) contributed the most to the model (Table A5.2). Lastly, the predicted distribution for the eastern grey squirrel was mostly described by bio 14 (Precipitation of Driest Month) and bio 3 (Table A5.2).

We found that the model with a human footprint (percentage contribution = 2.7%) did not contribute much to the potential distribution of the house mouse (Table A5.3, A5.4). Bio 3 still contributed the most in the potential distribution of the house mouse when the human footprint was included (Fig. A5.4), indicating that it has the most useful information by itself. The model had the AUC value of 0.78 for all the variables, lower than an AUC of 0.862 without the human footprint (Fig. A5.4). Both the projected models showed that the house mouse distribution is not likely in some areas of the Northern Cape, North West and Limpopo Provinces (Figs 5.2 and 5.3). However, the model with the human footprint shifted for some provinces, for example, Mpumalanga and KwaZulu-Natal (Figs 5.2 and 5.3). The human footprint was most important in predicting the distribution of the Norwegian rat, contributing 25% to the model (Table A5.3). This indicated that the human footprint had the most information not present in the other variables (Fig. A5.5). This species' potential distribution also expanded to the country's inner areas, with large suitability in Western Cape, Eastern Cape, Free State, KwaZulu-Natal, and Gauteng Provinces (Fig. 5.3). When the human footprint was added, the AUC value of the model was 0.90 (Fig. A5.5), lower than that with only the bioclimatic variables (AUC = 0.98).

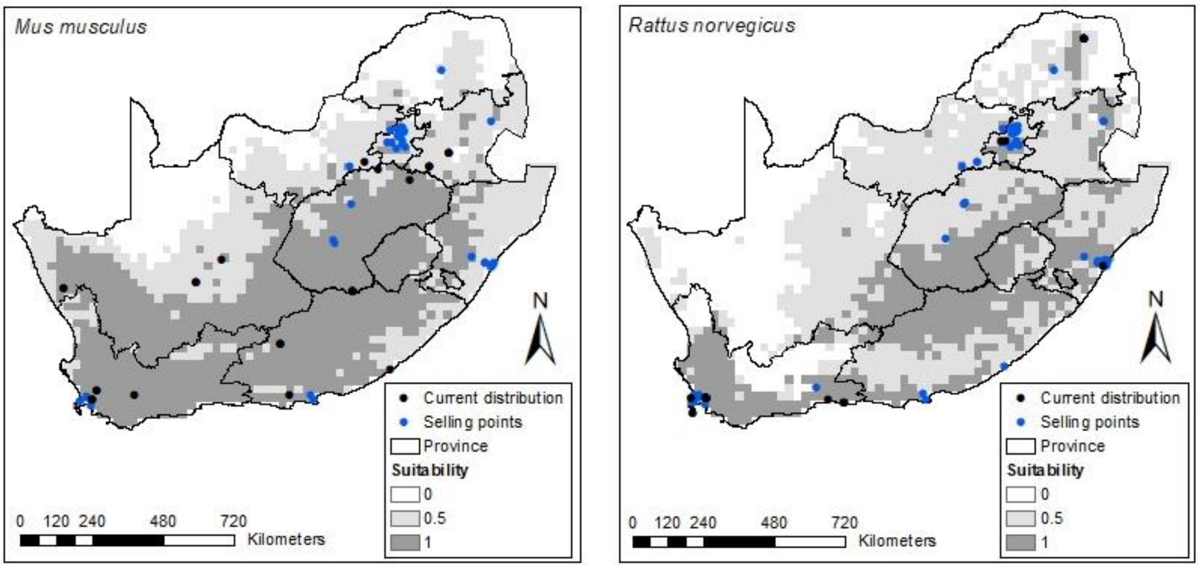

Fig. 5.3 The potential distribution of the house mouse (*Mus musculus*), and the Norwegian rat (*Rattus norvegicus*) predicted by species distribution model with the human footprint (Note: The colour ramp threshold on the right measured the suitability; dark grey indicates the most suitable areas, decreasing to light grey, and white being unsuitable).

A total of six species known to be invasive elsewhere through pet releases and escapes were found to have a potential distribution in South Africa (Fig. 5.4). The Guinea pig had the overall larger distribution of these species, covering Mpumalanga, Gauteng, Free State, KwaZulu-Natal and Eastern Cape (Fig. 5.4). Its distribution was also within the coastal areas of the Western Cape and off the coast in Northern Cape Province (Fig. 5.4). The model performed well in predicting this species' distribution with an AUC value of 0.824 (Table A5.2). Bio 3 and bio 14 contributed the most to the model for this rodent species (Table A5.2). The predicted suitability of the common marmoset, the black-tufted ear marmoset and the sugar glider was within the same provinces, covering the coastal areas of KwaZulu-Natal and Eastern Cape Provinces (Fig. 5.4). However, the distribution for the sugar glider extended to the coastal areas of Western Cape Province, while the common marmoset could distribute in the small section of Limpopo Province (Fig. 5.4). The AUC value for the black-tufted marmoset was

0.994, while that of the common marmoset and the sugar glider were 0.973 and 0.979 (Table A5.2). Bio 4 (Temperature Seasonality (standard deviation ×100)) and bio 3 contributed the most to the model for the common marmoset, while bio 3 and bio 18 (Precipitation of Warmest Quarter) were useful on the model for the black-tufted marmoset. For the sugar glider, the bioclimatic variables which contributed the most to the model were bio 3 and bio 14 (Table A5.2).

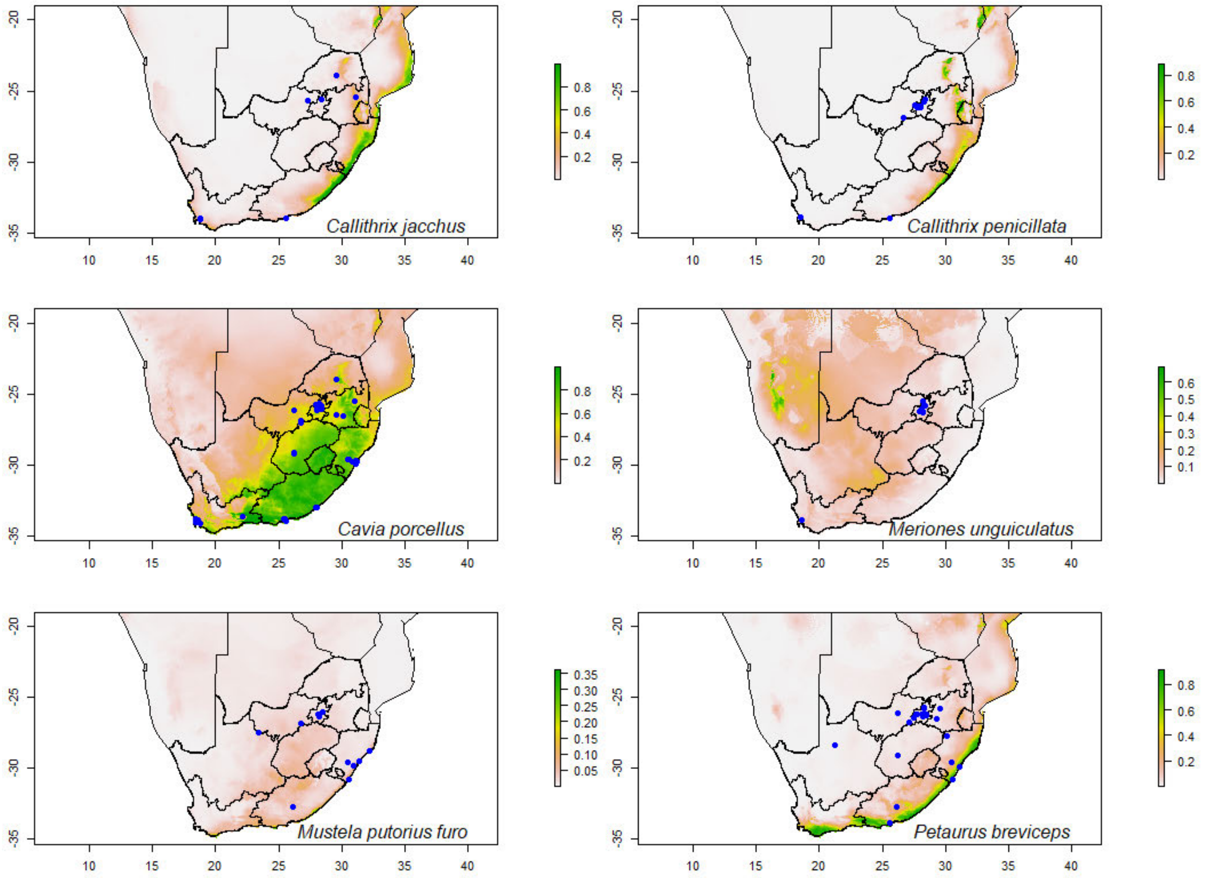

Fig. 5.4 The species distribution map of South Africa showing potential suitability for the common marmoset (*Callithrix jacchus*), the black-tufter ear marmoset (*Callithrix penicillata*), the Guinea pig (*Cavia porcellus*), the Mongolian gerbil (*Meriones unguiculatus*), the domesticated ferret (*Mustela putorius furo*), and the sugar glider (*Petaurus breviceps*). (Note: The colour ramp threshold on the right measured the climatic suitability; green indicates the most climatic suitable areas, decreasing to yellow, orange, with light gold and white being unsuitable).

The last two species, the Mongolian gerbil (*Meriones unguiculatus* (Milne-Edwards, 1867) and the domesticated ferret, had the lowest projected distribution. The distribution of the domesticated ferret was relatively large in the coastal areas of the Western Cape, Eastern Cape and KwaZulu-Natal Provinces (Fig. 5.4). For the Mongolian gerbil, the projected distribution was larger in the coastal areas of the Northern Cape Province (Fig. 5.4). The model performed well in predicting these two species, with an AUC value of 0.968 for the domesticated ferret and 0.761 for the Mongolian gerbil (Table A5.2). In terms of the bioclimatic variable contribution, bio 4 and bio 19 best described the potential distribution for the Mongolian gerbil, while bio 14 and bio 10 (Mean Temperature of Warmest Quarter) contributed the most on the model for the domesticated ferret (Table A5.2). We found that some of the selling points fell within the projected distribution for species such as the sugar glider, the common marmoset and the black-tufted ear marmoset (Fig. 5.4).

The last four species, except for the common squirrel monkey, are commonly available in the South African pet trade (Table 5.1). The common squirrel monkey had become invasive in Brazil through the accidental escape of pets (Table 5.1). We found that all these four species had potential distribution in South Africa (Fig. 5.5). However, the golden hamster (*Mesocricetus auratus* ((Waterhouse, 1839)) had the largest potential distribution, followed by the common squirrel monkey, the African pygmy hedgehog (*Atelerix albiventris* (Wagner, 1841)) and the common degu (*Octodon degus* (Molina, 1782)). In terms of distribution, the golden hamster would potentially distribute in the Western Cape, and including small sections of the Northern Cape, Eastern Cape, Free State and coastal areas of the KwaZulu-Natal Province (Fig. 5.5). The common squirrel monkey could potentially distribute in KwaZulu-Natal Province's coastal areas, extending to the Eastern and Western Cape Provinces (Fig. 5.5). The predicted distribution of the African pygmy hedgehog was within the small section of

Limpopo, Mpumalanga, KwaZulu-Natal and Western Cape Provinces (Fig. 5.5). Lastly, the common degu was projected to distribute in the small portion of the coast, including the inland of the Northern Cape and Western Cape Provinces (Fig. 5.5). We found that only the golden hamster had its selling points falling within its projected distribution (Fig. 5.5).

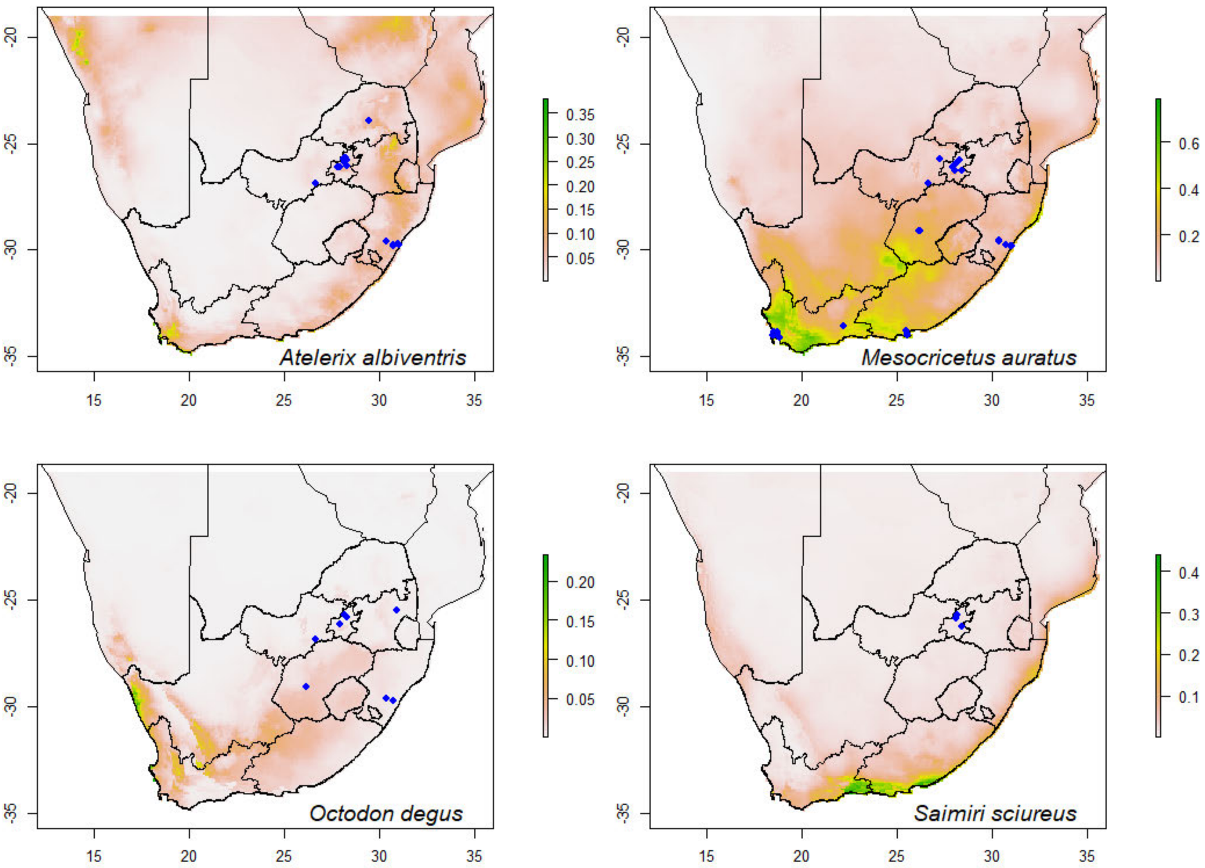

Fig. 5.5 The potential distribution maps showing the areas that are potentially climatically suitable for the African pygmy hedgehog (*Atelerix albiventris*), the golden hamster (*Mesocricetus auratus*), the common degu (*Octogon degus*) and the common squirrel monkey (*Saimiri sciureus*) in South Africa. (Note: The colour ramp threshold on the right measured the climatic suitability; green indicates the most climatic suitable areas, decreasing to yellow, orange, with light gold and white being unsuitable)

The model performed well in predicting the distribution of all the four species, with an AUC of 0.984 for the African pygmy hedgehog, 0.799 for the golden hamster, 0.948 for the common degu and 0.924 for the common squirrel monkey (Table A5.2). Bio 3 and bio 13 (Precipitation of Wettest Month) contributed the most to the model of the African pygmy hedgehog (Table A5.2). For the golden hamster, bio 19 and bio 4 contributed the most to the model, while bio 18 and 9 (Mean Temperature of Driest Quarter) contributed the most to the model for the common degu (Table A5.2). The potential distribution of the common squirrel monkey was best described by bio 19 and bio 4 (Table A5.2).

5.5 Discussion

Several species with distribution records in the present study are invasive in various countries, and the introduction of some of these species resulted from accidental escape and intentional releases from urban areas (Table 5.1). Cities and towns from which the potential climatic suitability of the studied species matched are considered to be at risk of becoming invaded as many introductions take place in the urban areas where pet stores are situated and where there is high human density (Banha et al., 2017; Filz et al., 2018). In addition, urban areas are regarded as hotspots of biological invasion as many introductions start there (Gaertner et al., 2017). Also, some species' selling points were within the projected highly suitable areas; consequently, such species may become invasive if released or escape captivity.

Our study found that very common small mammalian species in the South African pet trade had larger climatic suitability than rare species, such as the European rabbit, the sugar glider, the house mouse, and the Norwegian rat. The latter two have been introduced on all the continents except Antarctica (Musser & Carleton, 2005). These two rodent species are already invasive in South Africa and its offshore islands (Picker & Griffiths, 2017; Measey et al., 2020). On the mainland of South Africa, the Norwegian rat and the house mouse are distributed in

Gauteng, KwaZulu-Natal, Eastern Cape, Northern Cape and Western Cape Provinces. These small mammalian species have large areas that are climatically suitable in South Africa. In urban areas, invasive species such as the Norwegian rat and the house mouse are distributed in populated areas such as townships, especially in busy cities such as Durban, Johannesburg and Pretoria (Taylor et al., 2008; Bastos et al., 2011; Julius et al., 2018; pers. obs.). In addition, the human footprint was found to explain the suitability of the Norwegian rat. These results support that this species is commensal with humans, and its spread has been facilitated by socio-economic factors (Panti-May et al., 2016; Schweinfurth, 2020).

The human footprint did not explain the house mouse's distribution well; however, this does not indicate that it is not commensal as it is found in the cities (Phifer-Rixey et al., 2015; Williams et al., 2018). The predicted distributions of the house mouse were within the predicted suitability, but for the Norwegian rat, the distribution was in areas with low predicted suitability, for example, the Limpopo Province. This suggests that the human footprint rather than bioclimatic variables influence the distribution of the Norwegian rat more, as the results indicated that the Limpopo Province was suitable when the human footprint was added to the model. However, the distribution of the house mouse was explained more by the bioclimatic variables than the human footprint, as suggested by our results. These rodents pose a health risk to humans as they have been reported to carry several pathogens such as toxoplasmosis and leptospirosis (Taylor et al., 2008; Julius et al., 2018). These rodent species are also one of the most damaging agricultural pests worldwide, causing millions of dollars in damages and repairs (Pimentel et al., 2005; Almeida et al., 2013; Shivambu et al., 2020a).

In most countries and several islands, the house mouse and the Norwegian rat have been associated with the extinction of several native species through competition and predation (Harris, 2009; Dagleish et al., 2017). The introduction of the house mouse and the Norwegian rat is typically associated with the shipping trade in South Africa and other countries (Long, 2003; da Rosa et al., 2017; Measey et al., 2020). However, given that these two species are common in the pet trade, it is important that they are not released into the wild, especially in provinces where they are climatically suitable because they may establish feral populations as they tolerate a wide range of habitats. Svihla (1936) encountered a colony of albino pet rats living in a feral condition and interbreeding with wild rats in Honolulu, Hawaii. In South Africa, rats with colour patterns typical of laboratory and pet rats, e.g. black hooded, champagne and albino rats with red eyes, live in feral conditions, biting human babies and elders in Alexandra Township (Maligana, 2018). Additionally, in different countries, media reports have implicated pet owners intentionally releasing or abandoning rats into the wild (Williams, 2014; Robbins, 2015; Drevfjall, 2020; Forder, 2020). Consequently, such incidents could possibly be happening in South Africa but are not reported.

The two other small mammalian species recorded as invasive in South Africa are the European rabbit which is invasive on the offshore islands, and the eastern grey squirrel currently distributed in the Western Cape Province (de Villiers et al., 2010; Measey et al., 2020). The distribution of these two species in South Africa is associated with accidental releases and accidental escapes from captivity (Measey et al., 2020). Although the European rabbit is invasive on the offshore islands, it has relatively few presence records in the Gauteng and Western Cape Provinces. This indicates that this species is being released or has accidentally escaped captivity. The European rabbit and the eastern grey squirrel are also regarded among the most destructive small mammalian species. For example, the European rabbit competes with domestic animals for pasture, and they are also responsible for impacting native species through habitat destruction (Croft et al., 2002; Lees & Bell, 2008; Hume 2017). The eastern grey squirrel negatively affects forestry production, causing millions of dollars in damages and repairs (Lawton & Rochford, 2007; Signorile & Evans, 2007).

The distribution records for the European rabbit and the eastern grey squirrel overlapped with the predicted climatic suitability. The distribution of these species in South Africa should be expected to expand should they rely on the climate to establish. A study by Shivambu et al. (2020b) also found that the distribution records of invasive bird species in South Africa overlapped with the predicted climatic suitability. This may suggest that species whose distribution records overlap with predicted suitability might be relying on the climate to survive.

The current selling points for species such as the common marmoset, the black-tufted ear marmoset, the Guinea pig, the Mongolian gerbil, the domesticated ferret, and the sugar glider were within or in close proximity to the high predicted suitable distribution areas. Given that the occurrence records for the sugar glider are typically in tropical and subtropical environments in its native and invaded ranges (Long, 2003), the climate may be an important factor in establishing this species in South Africa, given that it has large climatic suitability. In addition, the sugar glider is a generalist, and in its invaded range, Tasmania, this species negatively affected the population of cavity-nesting birds through competition for nests and predation (Heinsohn et al., 2015; Allen et al., 2018). The bioclimatic variables may also play a role in the distribution of the domesticated ferret in South Africa. It was highly suitable for distribution in coastal areas as in its invaded range in New Zealand (Ragg, 1998; Davison et al., 1999). This suggests that the domesticated ferret may establish feral populations in the coastal areas of South Africa should they be introduced there. However, this species could occupy lowlands habitats as it is associated with them in western Europe and New Zealand, where it is invasive (Buckley et al., 2013). Habitat suitability predictions may need to be conducted to determine the potentially suitable habitat in South Africa. The domesticated ferret may negatively impact the biodiversity in the coastal areas in case they become successful invaders in South Africa. In New Zealand, the domesticated ferret became successful invaders because of lack of predators, and they have been reported to predate on native penguins and ground-nesting birds (Ratz et al., 1999; Bodey et al., 2011).

The distribution records are important in determining the climatic suitability of a species. However, it is essential to consider that species invasion depends not only on the climate but also on factors such as high reproductive rate, broad diet, and lack of predators in introduced areas (Moraes et al., 2019). For example, the common marmoset and the black-tufted ear marmoset invasive capacity may be explained by their ability to obtain secondary resources in times of scarcity during highly seasonal environments (Pontes & Soares, 2005; Braz et al., 2019). In Brazil, these two marmoset species and the common squirrel monkey have become invasive as a result of pet escapes and mistaken releases of seized pet animals (Camarotti et al., 2015; da Rosa et al., 2017). While these species occur in the same areas in Brazil (da Rosa et al., 2017), our results showed that the three monkeys' climatic suitability in South Africa was along the coastal areas. Warm temperature, isothermality, dry and wet seasons seem to explain the *Callithrix* species' climatic suitability in South Africa. Nevertheless, the common squirrel monkey suitability was explained by temperature seasonality. This indicates that the two marmosets could have the highest invasive potential in South Africa when compared with the common squirrel monkey. In addition, a study in Brazil also found that the climate for these species was determined by warmer temperatures (Braz et al., 2019). Previous studies found that marmosets can occupy and survive very degraded habitats because they have a broad diet, social flexibility and are successful breeders (Teixeira et al., 2015; Moraes et al., 2019). Given the advantage of these biological characteristics and a suitable climate, these species pose an invasion risk in South Africa.

Commonly traded species such as the Guinea pig and the golden hamster may pose an invasion in South Africa, given that they are traded in most provinces, and most of their selling localities were within the projected distribution. There is little information on the impacts associated with these two rodents; the only available literature is on the role of the Guinea pig in the extinction of the Laysan rail (*Zapornia palmeri* (Frohawk, 1892)) in Hawaii through habitat destruction (Hume, 2017). Other commonly traded species such as the African pygmy hedgehog and the common degu were not predicted to have a large distribution in South Africa. This could be explained by the limited number of distribution records for these species. Therefore, the climate may not influence their distribution should they escape or released from captivity. The climatic conditions for these species were explained by dry seasons and warm temperatures. This is in correspondence to their natural habitats, which include desert, bushy, steppes, harsh and arid environments (Hoefer, 1994; Nowak, 1999). Although some of the species were not commonly traded in the pet trade, they were found to negatively impact agriculture, for example, the Mongolian gerbil (see Shivambu et al., 2020a). The predicted climatic suitability for this species was very low, only covering a small portion of the Northern Cape Province. In addition, its current selling points were not within the predicted distribution. However, species with selling points outside the predicted suitable areas may need to be monitored, and their sales should be regulated so that they are not introduced to areas with predicted suitability.

5.6 Conclusions

We concluded that all the 14 assessed species have potentially suitable areas in South Africa and may pose an invasion risk should they escape or released from captivity. Although all the assessed species may need monitoring, of most concern are the common marmoset, the sugar glider, the domesticated ferret, the house mouse, the European rabbit, the eastern grey squirrel and the Norwegian rat. These species are likely to become invasive or expand their current distribution in South Africa because they have a suitable environment, high availability in the pet trade, and can tolerate wide climatic ranges. In addition, some of the selling points for these species were within highly predicted suitable areas. Also, the human footprint contributed the most to the predicted distribution of the Norwegian rat. Therefore, this species may further expand its current distribution in South Africa with humans' assistance through the pet trade. It is important that the current legislation on the sale of highly invasive species with known impacts be revised to protect the South African biodiversity and economy. The public should be educated about the negative impacts associated with non-native small mammals. If pet owners no longer interested in keeping their pets, they should be able to return the pets to the pet stores or take their pets to rescue clubs. The authority that issue permits should first determine the climatic suitability and potential impacts of traded species before approval. Species with potential high invasion risk should not be allowed to be traded in South Africa because negative impacts reported in other countries might occur in South Africa.

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5.8 Declarations

5.8.1 Conflict of interest

The Authors declare no conflict of interest nor competing interests.

5.8.2 Availability of data and material

Data for this study is available on request from the authors.

5.8.3 Authors' contributions

NS and CTD conceptualised and did the sample design. NS implemented the study. NS and TCS analysed the data. NS wrote the manuscript draft while TCS and CTD edited the manuscript before submission.

5.8.4 Ethical approval

Not applicable

5.9 References

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5.10 Appendices

Table A5.1 Species availability of the 24 non-native mammalian species recorded in the South African pet trade between September 2018 and September 2019. An asterisk (*) indicate species (n = 14) assessed based on criterion (see methods section).

Scientific name	**Common name**	**Species availability**	
		No. of pet store	**No. of online websites**
Atelerix albiventris (Wagner, 1841) *	African pygmy hedgehog	29	6
Callithrix jacchus (Linnaeus, 1758) *	Common marmoset	2	4
Callithrix penicillata (É.Geoffroy Saint-Hilaire, 1812) *	Black-tufted-ear marmoset	3	2
Cavia porcellus (Linnaeus, 1758) *	Guinea pig	70	3
Cebuella pygmaea (Spix, 1823)	Pygmy marmoset	0	1
Cebus capucinus (Linnaeus, 1758)	Panamanian white-faced capuchin	0	1
Chinchilla chinchilla (Lichtenstein, 1829)	Short-tailed chinchilla	15	2
Chinchilla lanigera (Molina, 1782)	Long-tailed chinchilla	14	2
Echinops telfairi (Martin, 1838)	Lesser hedgehog tenrec	9	3
Meriones unguiculatus (Milne-Edwards, 1867) *	Mongolian gerbil	10	2
Mesocricetus auratus (Waterhouse, 1839) *	Golden hamster	54	3
Mus musculus (Linnaeus, 1758) *	House mouse	68	2
Mustela putorius furo (Linnaeus, 1758) *	Domesticated ferret	2	2
Octodon degus (Molina, 1782) *	Common degu	18	1
Oryctolagus cuniculus (Linnaeus, 1758) *	European rabbit	101	3
Petaurus breviceps (Waterhouse, 1838) *	Sugar glider	3	3
Phodopus sungorus (Pallas, 1773)	Winter white dwarf hamster	59	3
Potos flavus (Schreber, 1774)	Kinkajou	0	2
Rattus norvegicus (Berkenhout, 1769) *	Norwegian rat	78	4
Saguinus midas (Linnaeus, 1758)	Red-handed tamarin	0	1
Saguinus oedipus (Linnaeus, 1758)	Cotton-top tamarin	0	1
Saimiri sciureus (Linnaeus, 1758) *	Common squirrel monkey	0	1
Sciurus carolinensis (Gmelin, 1788) *	Eastern grey squirrel	0	1
Vulpes zerda (Zimmermann, 1780)	Fennec fox	0	2

Table A5.2 Predictor variables, the percentage contribution (%) and AUC training values for the 14 non-native small mammalian species sold as pets in South Africa. The full description for each variable is written below the table.

Species names	**Distribution records**	**AUC**	**Bio 2**	**Bio 3**	**Bio 4**	**Bio 8**	**Bio 9**	**Bio 10**	**Bio 13**	**Bio 14**	**Bio 15**	**Bio 18**	**Bio 19**
Atelerix albiventris	284	0.984	3	**25**	16	1	0	5	**20**	12	0	10	8
Callithrix jacchus	310	0.973	3.5	**21.5**	**35**	4	0	5	7	12	2	0	10
Callithrix penicillata	301	0.994	4	**30.6**	0	6	12.4	0	11	5	0	**26**	5
Cavia porcellus	69	0.824	2	**35.2**	0	6	10.8	0	3	**34.3**	1	3.2	4.5
Meriones unguiculatus	180	0.761	8	7	**39**	0	0	20	2	1	3	5	**25**
Mus musculus	10672	0.799	0	20.3	**34.7**	1	0	3	2	0	2	0	**37**
Mesocricetus auratus	64	0.862	1.5	**43.7**	0	2.5	16.3	0	4	2.3	0	1	**28.7**
Mustela putorius furo	478	0.968	13	6	0	1	0	**19.5**	4.5	**44**	10.7	0	1.3
Oryctolagus cuniculus	946	0.948	0	8	0	1	**22**	0	0	0	4	**45**	20
Phodopus sungorus	128	0.944	3	17.7	**18.3**	1	0	12	2	10	9.7	1	**35.3**
Petaurus breviceps	1000	0.979	4	**52**	0	0	2	0	1	**28**	2	8	3
Rattus norvegicus	2615	0.97	3	**22**	0	2	11	0	1	14.2	3.8	6.8	**36.2**
Saimiri sciureus	837	0.924	1	**28**	0	0	3	0	3.1	16	1.9	5	**42**
Sciurus carolinensis	2048	0.98	13.7	**22.3**	0	0	0	0	6	**58**	0	0	0

Bio 2: Mean Diurnal Range (Mean of monthly (max temp - min temp)), **Bio 3**: Isothermality (BIO2/BIO7) (×100), **Bio 4**: Temperature Seasonality (standard deviation ×100), **Bio 8**: Mean Temperature of Wettest Quarter, **Bio 9**: Mean Temperature of Driest Quarter, **Bio 10**: Mean Temperature of Warmest Quarter, **Bio 13**: Precipitation of Wettest Month, **Bio 14**: Precipitation of Driest Month, **Bio 15**: Precipitation Seasonality (Coefficient of Variation), **Bio 18**: Precipitation of Warmest Quarter, **Bio 19:** Precipitation of Coldest Quarter

Table A5.3 Percent contribution of environmental variables for *Mus musculus* and *Rattus norvegicus* when the human footprint was added to the model.

Variables	*Mus musculus*	*Rattus norvegicus*
Bio 2: Mean Diurnal Range (Mean of monthly (max temp - min temp))	2.4	0.9
Bio 3: Isothermality (BIO2/BIO7) (×100)	42.7	22.2
Bio 4: Temperature Seasonality (standard deviation ×100)	0	4.4
Bio 8: Mean Temperature of Wettest Quarter	1.7	1.2
Bio 9: Mean Temperature of Driest Quarter	19.8	0
Bio 10: Mean Temperature of Warmest Quarter	0	8.3
Bio 13: Precipitation of Wettest Month	8.1	4.7
Bio 14: Precipitation of Driest Month	5.5	11.4
Bio 15: Precipitation Seasonality (Coefficient of Variation)	0.6	6.5
Bio 18: Precipitation of Warmest Quarter	0.3	0.8
Bio 19: Precipitation of Coldest Quarter	16.2	14.6
Human footprint	2.7	25

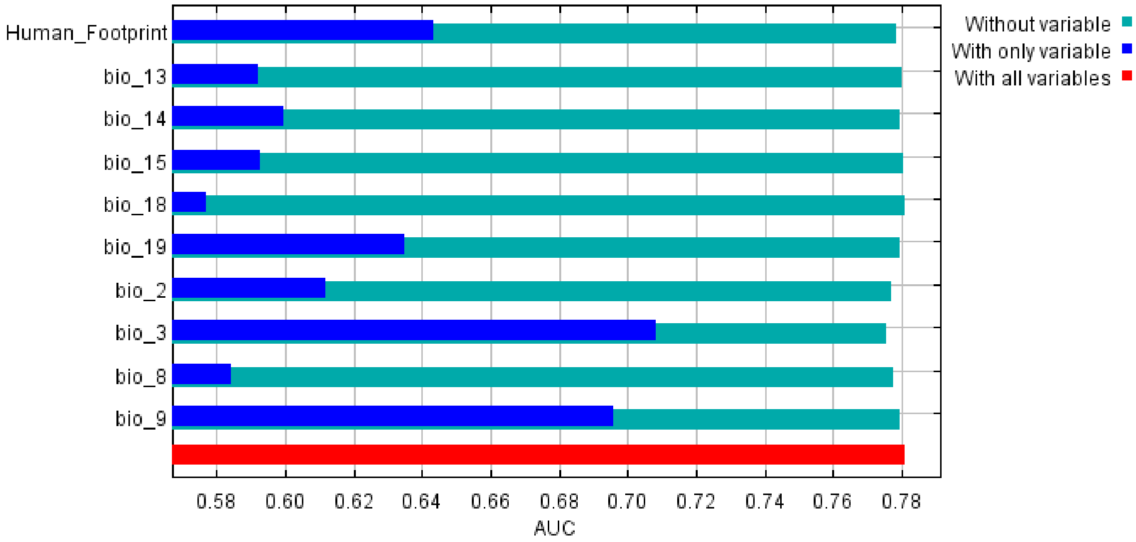

Fig. A5.4 Jack-knife results of area under the curve (AUC) of each individual variable used for *Mus musculus* predictions.

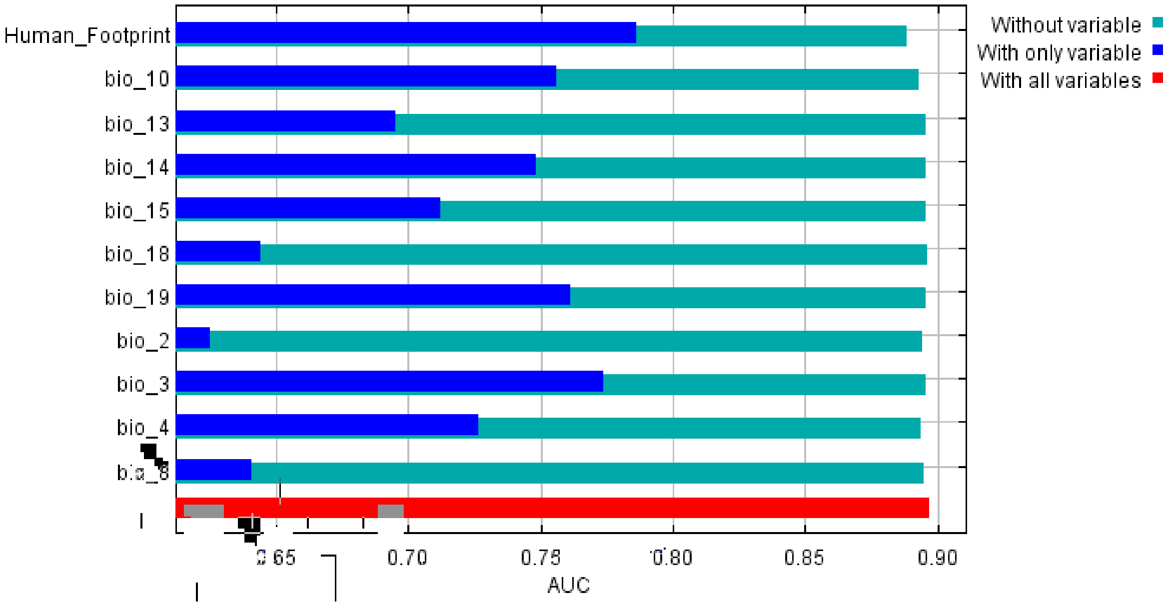

Fig. A5.5 Jack-knife results for the area under the curve (AUC) of each individual variable used for *Rattus norvegicus* predictions.

CHAPTER 6

Genetic diversity of non-native small mammal species sold in the South African pet shops

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6.1 Abstract

Murid rodent species have been introduced around the world for pet trade purposes, including food for other pets and companion animals. Species such as *Mastomys coucha*, *Rattus norvegicus* and *Mus musculus* pose an invasion and human health risk, as many zoonotic pathogens are associated with these three species. Little is known about the genetic diversity of captive rodent populations, and many species are incorrectly identified or mislabeled in the pet trade industry. In this study, mitochondrial gene regions were used to assess the taxonomy and genetic diversity of 156 pet rat and mouse samples from eight South African Provinces. A total of 115 specimens were identified as *M. musculus*, while 35 and six were *R. norvegicus* and *M. coucha*, respectively. Both separate and combined analyses revealed that the three species were monophyletic, but that there was genetic diversity within *M. musculus* and *R. norvegicus*. In particular, the combined data recovered 19 unique haplotypes for *M. musculus* and eight haplotypes for *R. norvegicus*. KwaZulu-Natal, Western Cape and Gauteng Provinces had more unique haplotypes when compared with other provinces. There were no clear geographically correlated genetic diversity patterns for *M. musculus,* but *R. norvegicus* did show some very subtle geographic structure. Non-native species were widely distributed in the South African pet trade industry, while the native *M. coucha* was not widely traded. This suggests that most of the provinces comply with the trade regulations on native species.

Keywords: Invasion; pet rodent; Mitochondrial DNA; trade patterns; management

6.2 Introduction

Many rodent species have been accidentally and intentionally introduced around the world through different anthropogenic-mediated pathways (Long 2003; Carpio et al. 2020). These pathways include transportation of goods (via aeroplanes, trains and ships), food, biological control, fur markets, aesthetics, research and the pet trade (Perry et al. 2006; Barun et al. 2011; Measey et al. 2020). Several rodent species have become invasive through these pathways, for example, the Gambian pouched rat *Cricetomys gambianus*, house mouse *Mus musculus*, and Norwegian rat *Rattus norvegicus* (Engeman et al. 2006; Measey et al. 2020). The latter two are amongst the most common small mammalian species kept as pets worldwide (Maligana et al. 2020; Mori et al. 2017; Lankau et al. 2018; Shivambu et al. 2021). These species are also sold as feeders for other non-native pets such as reptiles (snakes, lizards and turtles), amphibians (frogs and toads), and invertebrates (spiders) (Cooper and William 2014; Sincage and Hardin 2015; Cartwright et al. 2016; Kanagarajah et al. 2018; Rawski et al. 2018).

Mus musculus and *R. norvegicus* have been introduced to every continent except Antarctica (Berry 1968; Atkinson 1985; Vadell et al. 2014), although these pests have decimated the seabird population on several sub-Antarctic islands (Rowe-Rowe et al. 1989; Angel et al. 2009). These species play an essential role as agricultural pests around the world (Vadell et al. 2010; Stejskal et al. 2016). Both pet or wild rats and mice pose health risks to humans as they spread zoonotic diseases such as salmonellosis and rat-bite fever (Stehle et al. 2003; Harker et al. 2011; Rabiee et al. 2018). They also cause damage to roof voids, electric cables, and clothes by gnawing on them (Sidorov and Putin 2010; Yonas et al. 2010; Garba et al. 2014; Panti-May et al. 2017). *Mus musculus* and *R. norvegicus* have also been implicated in the extinction of several reptiles, bird, and insect species on different islands through predation (Marris 2000; Cuthbert and Hilton 2004; Dagleish et al. 2017). The invasion success of these two rodents is linked to human habitation as they exploit these habitats for food and shelter (Sacchi et al. 2008; Vadell et al. 2010).

In South Africa, *R. norvegicus* and *M. musculus* distributions are associated with high-density urban areas (Taylor et al. 2008; Bastos et al. 2011). The introduction of *M. musculus* has been linked with the early shipping to South Africa, while *R. norvegicus* is thought to have arrived via Asian and European shipping routes (Measey et al. 2020). Today, these non-native rodent species dominate the pet trade industry as they are sold as both pets and feeders in the country (Maligana et al. 2020). Native rodent species such as the Natal multimammate mouse *Mastomys natalensis* and southern multimammate mouse *Mastomys coucha* are also used for pet trade purposes in South Africa (du Plessis et al. 2016). Tracking trade in these species is complicated because *Mastomys natalensis* and *M. coucha* are similar morphologically but can be accurately distinguished using molecular analysis (Bastos et al. 2005; Kneidinger et al. 2014).

Most of the species are incorrectly identified or mislabeled in the pet trade industry as a result of cryptic species and the lack of taxonomic expertise by the traders (Gerson et al. 2008; Sanders et al. 2008; Gehring et al. 2018; Shivambu et al. 2020; Nelufule et al. 2020; Maligana et al. 2020). Consequently, the lack of correct taxonomic information of traded species poses challenges in enforcing regulations regarding their shipment into a foreign country (Lankau et al. 2017). In addition, accurate species identification is important for effective conservation, especially for endangered species, which may be traded as pets (Nagy et al. 2012; Wenner et al. 2012; Mishra et al. 2017). Taxonomic uncertainty also limits the ability to document the true scale of species utilised in the pet trade industry (Strecker et al. 2011; Ng et al. 2016).

Presently, the populations of *M. natalensis*, *M. coucha*, *R. norvegicus* and *M. musculus* are not threatened by the pet trade industry as they are listed as least concern (Cassola 2016;

Granjon 2016; Musser et al. 2016; Ruedas 2016). However, these species' trade poses a health risk to humans as they are reservoirs for zoonotic diseases (Bastos et al. 2005; Skinner and Chimimba 2005; Lecompte et al. 2006; Harker et al. 2011; Rabiee et al. 2018). In addition, non-native rodents may become invasive through pet trade releases and escapes in South Africa. For example, Maligana (2018) observed colonies of red-eyed albino rats typical of laboratory and pet rat strain living in feral conditions in Alexandra township, South Africa. Julius (2013) also revealed that *R. norvegicus* haplotype was closely linked to both wild and laboratory strain, suggesting possible introduction from Indonesia by escaped laboratory rats, subsequently forming a distinctive haplotype in South Africa. This suggests that these rats may have high genetic diversity that may increase their establishment, spread, and adapt to new habitations, as reported for other invasive species with high genetic variation (Stepien et al. 2005). Assessing the genetic structure of non-native species is useful in determining the origin or source of the introduced populations and in evaluating the rate of invasion success (Collins et al. 2002; Campbell et al. 2019). In this study, we used four mitochondrial markers to identify and assess the genetic diversity of captive rodent populations in South Africa. We also investigated the geographic distribution pattern of rodent species genetic diversity to determine breeding stock sources. We predicted that there is genetic diversity within the rodent species sold in South African pet shops, and their genetic diversity follows a clear geographically correlated pattern.

6.3 Materials and methods

6.3.1 Sample collection

Pet shops sell frozen and live rodents as food for predator pets such as snakes, lizards and tarantulas. We purchased between two to five frozen mice and rats from each of the 122 pet shops across South African provinces (Fig 6.1). Frozen rodents were used instead of living rodents because of ethical restrictions, but the same rodents are bred for both feeding and pet purposes (N Shivambu 2019, pers. comm.). Rodent samples were sealed in zip-up bags, stored in a car portable fridge, and transported to the University of KwaZulu-Natal for analyses.

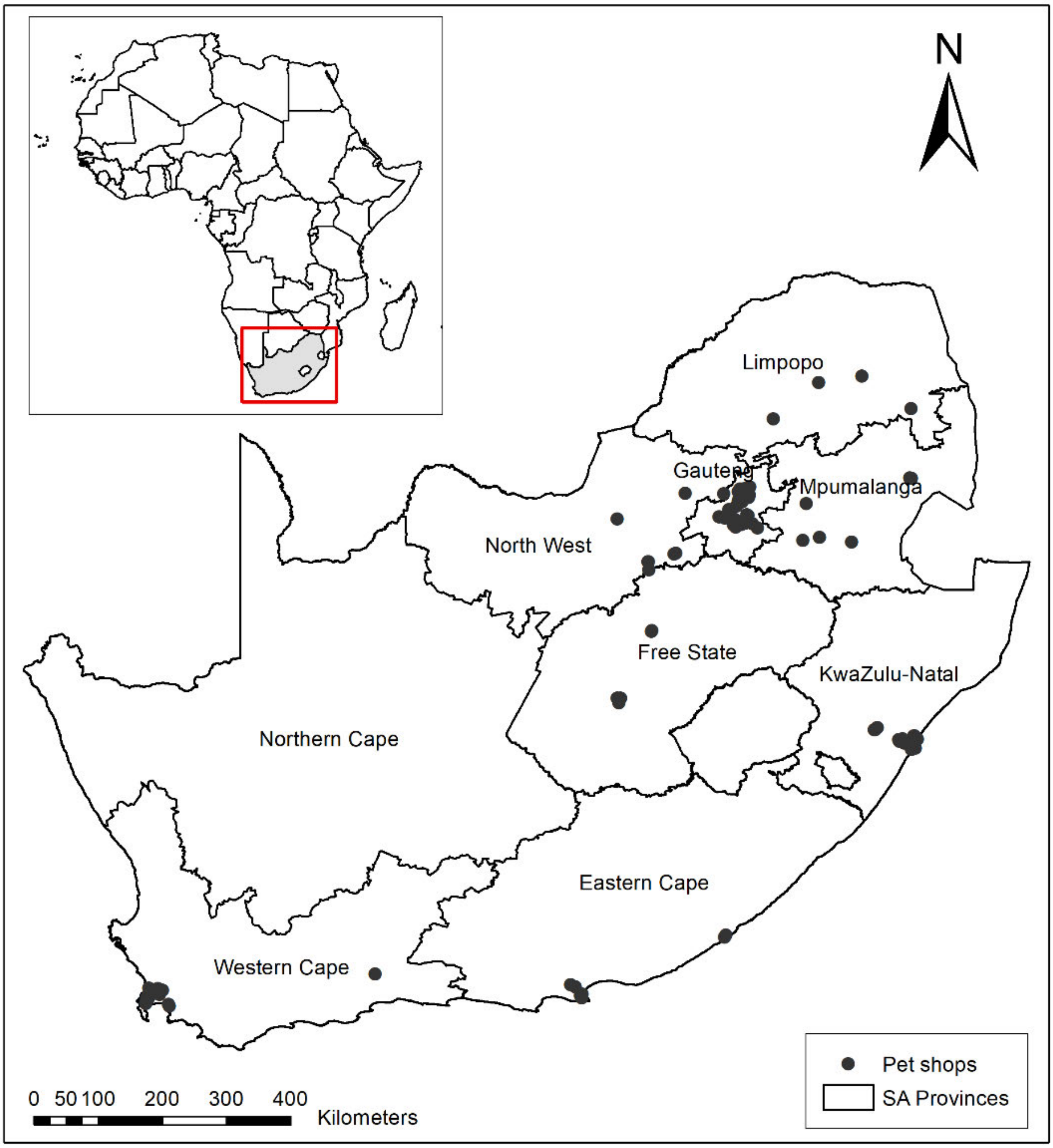

Fig. 6.1 A map of South Africa showing the physical pet shop locations from where pet rodents were sampled in September 2020.

6.3.2 DNA extraction and Polymerase Chain Reaction (PCR)

Tissue samples from the specimens were dissected using surgical blades and forceps. We used disposable scalpels and disinfected them with 99% ethanol and flame to avoid contaminations. We harvested liver tissue from each individual and stored these in respective 1.5ml Eppendorf tubes filled with 99% ethanol for molecular analyses. Genomic DNA was extracted from 156 rat and mice tissue liver samples using the Omega Bio-tek extraction Kit (Norcross, Georgia) following the manufacturer's standard protocol. The extracted DNA was stored in a -80 °C freezer until further analyses. DNA extracts were amplified by PCR targeting four mitochondrial gene regions: Cytochrome *b* (C*yt-b),* cytochrome oxidase subunit 1 (*CO1*), 16S ribosomal RNA (16S rRNA) and the hypervariable control region (CR). These gene regions were chosen as they have been reliably used to resolve mammalian phylogenies (Pun et al. 2009; Nicolas et al. 2010). The PCRs were done in a reaction volume of 14.5 μl containing 5.25 μl of double-distilled water (ddH_2O), 6.25 μl OneTaq® – 2X Master Mix with Standard Buffer (New England Biolabs, Ipswich, MA, USA) or EmeraldAmpMax PCR Master Mix (Takara Bio Inc, Kusatsu, Shiga, Japan), 0.5 μl of each oligonucleotide primer and 2 μl DNA template. Each set of PCR reactions included a negative control (no template control) to detect contamination of reagents. PCR products were visualised on 1.5% TBE agarose gel, and we used Quick-Load® 1 kb DNA Ladder (New England Biolabs) to estimate the size of amplicons. The primer details, cycling conditions and the size of the amplified fragment for each gene region are listed in Table 6.1. For Sanger sequencing, PCR products were sent to Central Analytical Facility (CAF) at Stellenbosch University, or KwaZulu-Natal Research Innovation and Sequencing Platform (KRISP), at the University of KwaZulu-Natal, South Africa. All sequences were BLASTed against the NCBI GenBank database (www.ncbi.nlm.nih.gov/blast) to verify sequences. The cut-off threshold for species identification in GenBank was chosen based on reference sequences similarities ranging from 90–100%.

Table 6.1 Details of primers used to amplify each gene region in the current study. The size of the amplified PCR fragment and details of cycling conditions used are also provided. References for primers used are provided below the table

Region	**Primer name**	**Primer sequence (5'-3')**	**Amplified fragment size**	**PCR conditions**
C*yt-b* **(**1**)**	L14723 (F) H15915 (R)	CCA ATG ACA TGA AAA ATC ATC GTT TCT CCA TTT CTG GTT TAC AAG AC	890 bp	1. 96 ºC for 20 s 2. 96 ºC for 12 s, 49 ºC for 25 s, 72 ºC for 60 s (X2) 3. 96 ºC for 12 s, 47 ºC for 20 s, 72 ºC for 55 s (X5) 4. 96 ºC for 12 s, 45 ºC for 15 s, 72 ºC for 50 s (X35) 5. 72 ºC for 1 minute
CO1 **(**2**)**	LCO1490 (F) HCO2198 (R)	GGT CAA CAA ATC ATA AAG ATA TTG G TAA ACT TCA GGG TGA CCA AAA AAT CA	637 pb	1. 94 ºC for 1 minute 2. 94 ºC for 30 s, 50 ºC for 30 s, 72 ºC for 60 s (X35) 3. 72 ºC for 10 minutes
16S rRNA **(**3**)**	16SA (F) 16SB (R)	CGC CTG TTT ATC AAA AAC AT CCG GTC TGA ACT CAG ATC ACG T	433 bp	1. 94 ºC for 2 minutes 2. 94 ºC for 30 s, 50 ºC for 45 s, 68 ºC for 60 s (X35) 3. 68 ºC for 5 minutes
CR **(**4**)**	N777 (F) DLH1 (R)	TAC ACT GGT CTT GTA AAC C ATC CTC TCT CTG CAG CAC ATT TCC	433 bp	1. 94 ºC for 3 minutes 2. 94 ºC for 30 s, 48 ºC for 30 s, 68 ºC for 1:30 s (X35) 3. 68 ºC for 10 minutes

References: [1] Ducroz et al. 2001, [2] Folmer et al. 1994, [3] Palumbi et al. (1991), [4] Alpers et al. 2004

6.3.3 Phylogenetic analyses

We edited sequence chromatograms and aligned each gene region separately using ClustalW 2.0 (Larkin et al. 2007). After computational alignment, sequence alignments were manually optimized in BioEdit 7.2.6 (Hall 2005) to ensure homology. We estimated the length of each final alignment, the number of conserved sites, and the number of parsimonious sites in Mega 6 (Tamura et al. 2013). Haplotype number (h), Haplotype diversity (HD), and nucleotide diversity (π; SD) were estimated using DnaSP 5.10.1 (Rozas et al. 2017). The sequences generated in the present study were deposited in GenBank (accession numbers: MZ353018-MZ353519).

We constructed phylogenies using two model-based methods, maximum likelihood and Bayesian inference. The best-fit substitution model for each gene region was selected based on the Akaike information criterion (AIC) using JModeTest 2.1.6 (Darriba et al. 2012) on the CIPRES server (Miller et al. 2010). The best-fitting substitution models were GTR for C*yt-b*, Tim3+G for *CO1*, Tim2+G for 16S rRNA and Tpm3uf+I for CR. We conducted phylogenetic analyses on each gene region separately, thereafter we combined the sequence data for the four mitochondrial markers into a single dataset and inferred the phylogeny using a partitioned approach. Phylogenies from the analyses of individual gene regions were compared for conflict before the combined analyses were conducted.

We performed maximum likelihood analyses (ML) using Garli 2.0 (Zwickl 2006). MrBayes 3.2.7a (Ronquist et al. 2012) was used to conduct Bayesian inference (BI). Both programmes were run on the CIPRES server. For maximum likelihood, branch support was assessed using 1000 bootstrap replicates. Consensus trees were constructed using the 50% majority rule method in CONSENSE in the PHYLIP package (Felsenstein, 2005).

For the BI, two independent runs, each consisting of four Markov Monte Carlo chains (MCMC), were run for 20 million generations. To confirm the convergence of MCMC chains, Tracer 1.7 (Rambaut et al. 2018) was used. Thereafter, 20% of initial trees were removed as burn-in from the tree file before consensus trees were constructed. Branch support was assessed using posterior probability values. All trees (ML and BI) were midpoint rooted, and bootstrap and posterior probability values were annotated onto the most likely tree.

We also used haplotype networks to examine the genetic diversity of rodents. We conducted median-joining network analysis for each gene region and the combined dataset using PopART 1.7 (Leigh and Bryant 2015).

6.4 Results

6.4.1 Genetic diversity

Using BLAST search results, 156 sequences were identified as *Mus musculus* (number of sequences (n) = 115), *Rattus norvegicus* (n = 35) and *Mastomys coucha* (n = 6). The nucleotide composition and genetic variables for each species differed for the four gene regions (Table 6.2). The most variable mtDNA region was the *CO1* in *M. coucha* (6 variable characters) and *M. musculus* (33 variable characters), while *Cyt-b* was the most variable gene region in *R. norvegicus* (20 variable characters). The most conservation mtDNA region was 16S rRNA with the least number of variable characters in all three species. The final aligned data set, including all three rodent species, was 2485 bp in length. The combined dataset for *M. coucha* had eight variable sites, while *M. musculus* had 76 variable sites and 33 parsimonious sites. Lastly, the combined dataset for *R. norvegicus* had 27 variable sites and ten parsimonious sites (Table 6.2).

Table 6.2 Genetic variability of the mitochondrial DNA regions (16S rRNA, *CO1*, and *Cyt-b*), hypervariable control region (CR) and combined dataset of the rodent species sold in the South African pet shops

Variables	***Mastomys coucha***					***Mus musculus***					***Rattus norvegicus***				
	16S rRNA	***CO1***	***Cyt-b***	**CR**	**Combined**	**16S rRNA**	***CO1***	***Cyt-b***	**CR**	**Combined**	**16S rRNA**	***CO1***	***Cyt-b***	**CR**	**Combined**
Total number of individuals	5	5	6	6	6	112	71	93	112	112	34	2	25	31	34
Total base pair	525	637	890	433	2485	525	637	890	433	2485	525	637	890	433	2485
Conservative site	506	620	888	425	2439	504	604	868	417	2393	502	619	870	424	2415
Variables sites	0	6	0	2	8	9	33	22	12	76	3	0	20	4	27
Parsimonious informative sites	0	0	0	0	0	4	13	9	7	33	1	0	6	3	10
Singleton site	0	6	0	2	8	5	20	13	5	43	2	0	14	1	17
Nucleotide composition (%)															
T (%)	28.1	30.0	27.8	31.9	29.5	30	29.7	30	30.1	30.0	27.5	29.7	27.6	31.5	29.1
C (%)	19.2	26.0	26.7	26.8	24.7	18.3	24.7	26.7	25.2	23.7	19.3	26.8	30.3	25.8	25.6
A (%)	33.7	29.4	32.5	30.9	31.6	32.4	29.8	30.6	33.3	31.5	33.9	27.8	29.4	31.0	30.5
G (%)	19.0	14.6	13.0	10.4	14.3	19.3	15.8	12.7	11.4	14.8	19.3	15.7	12.6	11.7	14.8

For *M. musculus*, DnaSP analysis recovered more haplotypes in *COI* and *Cyt-b* genes, 15 and 11, respectively (Table 6.3). The genetic diversity for both these gene regions was 0.56, with *CO1* having higher nucleotide diversity than *Cyt-b* (Table 6.3). The combined data set for *M. musculus* recovered a total of 19 unique haplotypes, with 0.74 haplotype diversity and low nucleotide diversity (*P* = 0.002) (Table 6.3). Tajima's D was negative for all the gene regions except for CR in *M. musculus*, but it was not significant when all the mtDNA regions were combined (Table 6.3). For *R. norvegicus*, DnaSP analysis recovered more haplotypes in the *Cyt-b* gene, with a total of eight unique haplotypes. The haplotypic diversity was 0.76, with a low nucleotide diversity (*P* = 0.004) (Table 6.3). The same analysis recovered a total of eight unique haplotypes when the data set was combined. The haplotypic diversity (Hd = 0.76) was similar to *Cyt-b*; however, the nucleotide diversity (*P* = 0.003) was lower (Table 6.3). Tajima's D was negative for *Cyt-b*, but positive for 16S RNA, CR and combined data, but it was not significant (*P* = 0.97) (Table 6.3).

Table 6.3. Genetic diversity indices for two rodent species (*Mus musculus* and *Rattus norvegicus*) sold in South African pet shops based on mitochondrial DNA gene regions (16S rRNA, CO1, and ***Cyt-b***), hypervariable control region (CR) and combined dataset

	Number of individuals (*n*)	**Number of haplotypes (h)**	**Haplotype diversity (Hd)**	**Nucleotide diversity (π (SD))**	**Tajima's D**
Mus musculus					
16S rRNA	112	5	0.27	0.001	-0.09 (*P* > 0.10)
CO1	71	15	0.56	0.003	-1.88 (*P* > 0.05)
Cyt-b	93	11	0.56	0.001	-1.75 (*P* > 0.05)
CR	112	3	0.26	0.003	0.11 (*P* > 0.05)
Combined	51	19	0.74	0.003	-1.55 (*P* > 0.10)

	Number of individuals (*n*)	Number of haplotypes (h)	Haplotype diversity (Hd)	Nucleotide diversity (*π* (SD))	Tajima's D
Rattus norvegicus					
16S rRNA	31	2	0.49	0.0009	1.47 (*P* > 0.10)
Cyt-b	25	9	0.76	0.004	-0.79 (*P* > 0.10)
CR	31	3	0.52	0.002	0.91 (*P* > 0.10)
Combined	21	8	0.76	0.003	0.76 (*P* > 0.10)

6.4.2 Phylogenetic analyses

The phylogenies produced by maximum likelihood and Bayesian analyses were consistent; as a result, the most likely phylogeny was used to display bootstrap and BI support values. The phylogenies for both the separate and combined datasets revealed three distinct clusters belonging to *M*. *musculus*, *R*. *norvegicus* and *M*. *coucha* (Fig. 6.2; Supplementary Information Fig. S6.1–4). The three species formed single monophyletic clades on the tree topologies for 16S rRNA, *COI*, *Cyt-b*, CR and combined datasets (Fig. 6.2; Fig. S6.1–4). All three monophyletic clades were supported with high bootstrap support values in all phylogenies (Fig. 6.2; Fig. S6.1–4). The 16S RNA phylogeny revealed a total of eight different *M*. *musculus* genotypes and two different for *R*. *norvegicus* genotypes (Fig. S6.1). The *CO1* gene region phylogeny recovered 21 different genotypes for *M*. *musculus* and a single genotype for *R*. *norvegicus* (Fig. S6.2). In *Cyt-b* phylogeny, *M*. *musculus* had 11 different genotypes, while *R*. *norvegicus* had eight different genotypes (Fig. S6.3). In the CR gene region, the phylogeny recovered three different genotypes for *M*. *musculus* and *R*. *norvegicus* (Fig. S6.4). The combined datasets recovered a total of 21 different *M*. *musculus* genotypes, eight different *R*. *norvegicus* genotypes and a single genotype for *M*. *coucha* (Fig. 6.2). The genotypes for both *M*. *musculus* and *R*. *norvegicus* were separated into two well-supported clades (Fig. 6.2).

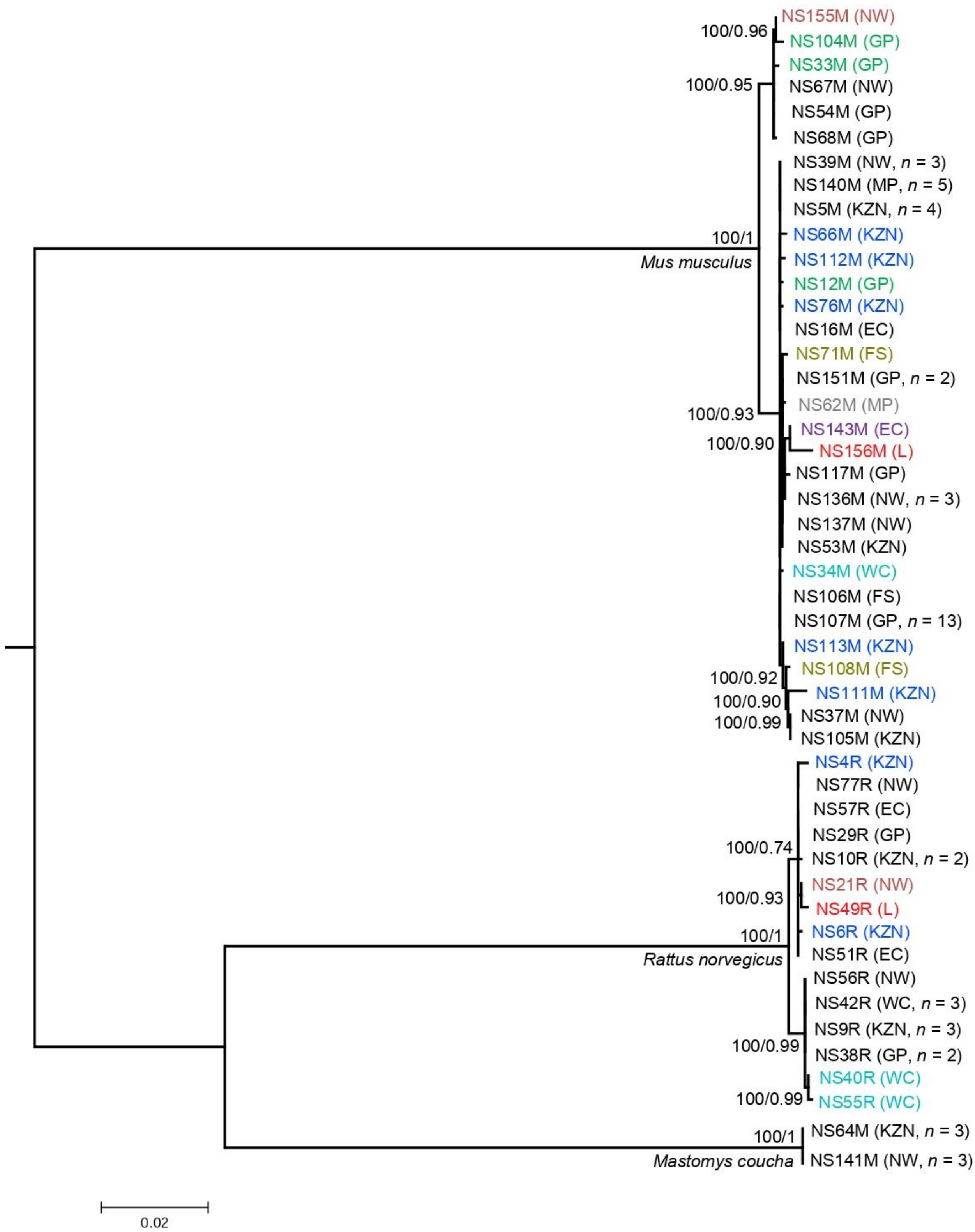

Fig. 6.2 Most likelihood phylogeny constructed from the combined data from four mtDNA gene regions, 16S ribosomal RNA (16S rRNA), cytochrome oxidase subunit 1 (*CO1*), mtDNA Cytochrome *b* (C*yt-b)*, and hypervariable control region (CR). The phylogeny includes *Mus musculus*, *Rattus norvegicus*, and *Mastomys coucha* collected from South African pet shops.

Nodal support values on branch nodes denote the maximum likelihood bootstrap (>50%) and Bayesian posterior probability (>0.6) support values. The number of identical sequences is shown in parentheses, and the colour coded taxa show unique individuals. The provinces where samples were collected are abbreviated as follows: EC - Eastern Cape, FS - Free State, GP - Gauteng Province, KZN - KwaZulu-Natal, L - Limpopo, MP - Mpumalanga, NW - North West, and WC - Western Cape

6.4.3 Haplotype network

Below species diversity was limited within *Mastomys coucha*, and haplotype networks were not constructed for this species. *Mus musculus* haplotype analysis showed that *CO1* and *Cyt-b* genes had more different nucleotides between haplotypes when compared with haplotypes in 16S RNA and CR. The most abundant haplotype, NS106M appeared to be the parent haplotype in 16S RNA, *Cyt-b*, *CO1* and CR data (Supplementary Material Fig. S6.5). Haplotype, NS54M was also ancestral to other unique haplotypes represented by five provinces (Supplementary Material Fig. S6.5). However, some of the haplotypes grouped together with this haplotype were separated in *Cyt-b* (Supplementary Material Fig. S6.5). Interestingly, *Cyt-b* had an additional abundant haplotype, NS136M, which was the parent haplotype for Mpumalanga Province haplotype, NS62M (Fig. 6.3). Gauteng, North West and KwaZulu-Natal Provinces had the most number of haplotypes in 16S RNA, *Cyt-b*, *CO1* and CR gene regions (Fig. 6.3).

The analysis of *M*. *musculus* combined dataset recovered a starburst haplotype network (Fig. 6.3). There was no clear geographically correlated pattern. The central haplotype (NS106M) was present in all provinces except Limpopo (Fig. 6.3). Another common haplotype was NS136M, which was found in six individuals, but this haplotype was only recorded from the North West and Gauteng Provinces (Fig. 6.3). A unique haplotype from Limpopo Province was distantly linked by eight mutational steps to this haplotype. KwaZulu-Natal Province had a high number of unique haplotypes (n = 7), of these, five were not found in any of the other provinces (Fig. 6.3). KwaZulu-Natal Province also shared a unique haplotype, NS105M, with Western Cape Province. The haplotypes for KwaZulu-Natal Province were all closely related, with haplotypes separated by single mutations, except for haplotype NS66M and NS111M, which were separated from other haplotypes by two and eight mutational steps, respectively (Fig. 6.3). Gauteng Province had six haplotypes, of which two were shared with North West Province (Fig. 6.3). The haplotypes shared with the North West Province were separated by single and 19 mutational steps (Fig. 6.3).

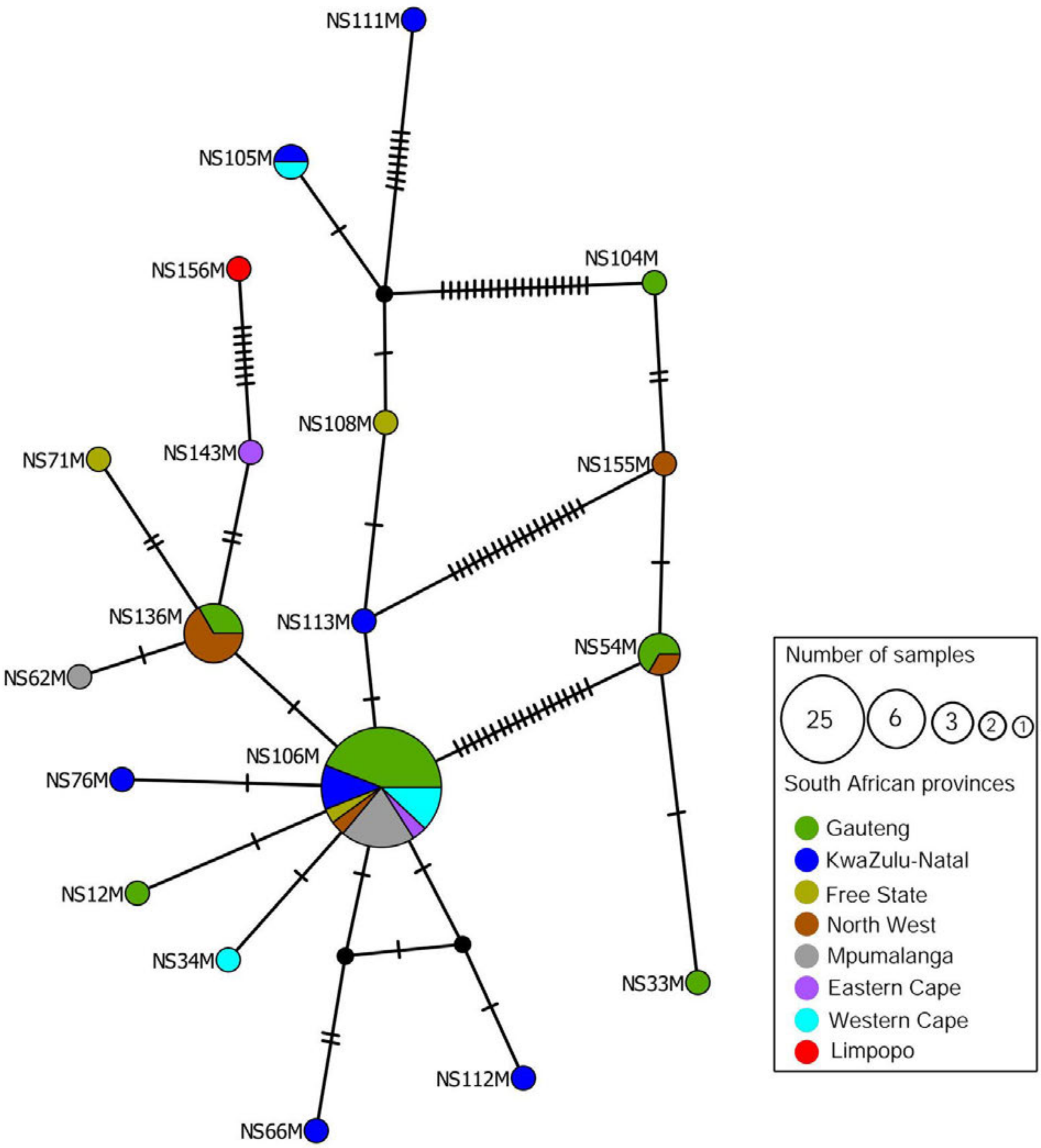

Fig. 6.3 Median-joining haplotype network constructed using combined data from four mtDNA gene regions (16S rRNA, CO1, Cyt-b and CR) based on 51 sequences of *Mus musculus* sold in South African pet shops

According to the haplotype network analysis for *R. norvergicus*, *Cyt-b* gene region had more different nucleotides between haplotypes when compared with 16S RNA and CR. NS10R appeared to be the parent haplotype in 16S RNA, *Cyt-b* and CR genes (Supplementary Material

Fig. S6.6). Another common haplotype, NS42R was shared by KwaZulu-Natal, Western Cape and Gauteng Provinces in all the three gene regions (Supplementary Material Fig. S6.6). In *Cyt-b* gene, NS42R was the parent haplotype for the three Western Cape Province unique haplotypes, separated by single and six mutational steps (Supplementary Material Fig. S6.6). Haplotype NS10R was separated by a single mutational step in 16S RNA, while in *Cyt-b* and CR, it was separated by five and two mutational steps, respectively. Western Cape and KwaZulu-Natal Provinces had more unique haplotypes in *Cyt-b* than in 16S RNA and CR (Supplementary Material Fig. S6.6).

The analysis of *R. norvegicus* combined dataset recovered a total of eight unique haplotypes, which showed a subtle geographic structure (Fig. 6.4). NS10R and NS42R were present in four provinces (Fig. 6.4). NS10R was the ancestral haplotype to two KwaZulu-Natal Province haplotypes and North West Provinces haplotypes. The North West Province haplotype, NS21R, was the ancestral haplotype to a Limpopo Province haplotype NS49R (Fig. 6.4). These haplotypes were separated from NS10R by single, two and three mutational steps. NS42R was the ancestral haplotype to two unique Western Cape Province haplotypes, separated by a single mutation. For *R. norvegicus* data, KwaZulu-Natal and Western Cape Provinces had more unique haplotypes when compared with other provinces (Fig. 6.4).

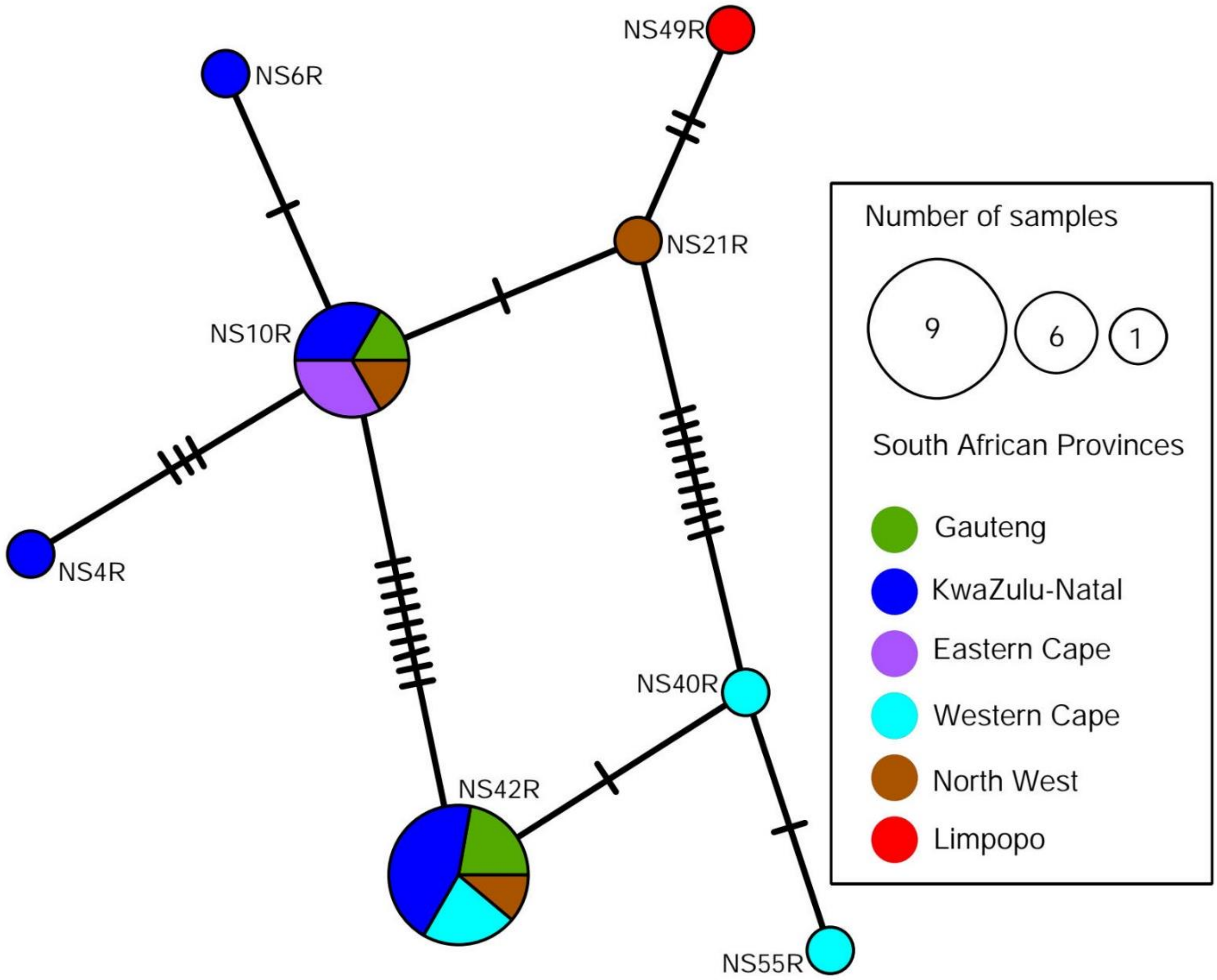

Fig. 6.4 Median-joining haplotype network constructed using combined data from three mtDNA gene regions (16S rRNA, *Cyt-b* and CR) based on 21 sequences of *Rattus norvegicus* sold in South African pet shops

6.5 Discussion

Four mitochondrial DNA gene data were used to identify and assess the genetic variation of the captive rodent populations in South African pet shops. Three species, including *M. musculus*, *R. norvegicus* and *M. coucha* were identified. The latter is native to South Africa, and it has been reported to be used for pet trade purposes with morphologically similar *M. natalensis* (du Plessis et al. 2016). However, our study only found that *M. coucha* was only available for sale in two provinces. The identification of *Mastomys* species is impossible based on the morphological appearance, but molecular analyses are useful in identifying this rodent species (Kruppa et al. 1990; Smit et al. 2001). It is possible that only *M. coucha* is sold and not *M. natalensis*, given that there are limited studies that identified rodent species sold in the South African pet shops based on molecular analysis. Again, a previous study by Kruppa et al. (1990) in Germany found that experimental animals assumed to be *M. natalensis* were all identified as *M. coucha*.

Based on the phylogenetic analysis, *M. coucha* was not widely sold when compared with the non-native *M. musculus* and *R. norvegicus*, which were sold in more than five provinces. This may be explained by that pet shop owners are not permitted to sell or breed South African native species, specifically endangered species (DEA 2016). According to the phylogenies in separate and combined dataset, *M. musculus* and *R. norvegicus* formed monophyletic clades. Both of these species exhibited below-species genetic diversity when compared with laboratory *M. musculus* and *R. norvegicus* strains (Song et al. 2014; Brekke et al. 2018). However, their genetic diversity was relatively high when compared to other laboratory rodent species, except ongolian gerbil *Meriones unguiculatus* (Brekke et al. 2018). This indicated that the pet shop owners breed or source different rat and mouse varieties, therefore may have led to the sampling of genetically different populations. In addition, there are more than 20 laboratory rat and mouse strains used in laboratories around the world (Tsang et al. 2005; Aitman et al. 2008; Atanur et al. 2013). As a result, some of these strains could have been introduced to the pet trade industry as most pet rats and mice are donated to pet shops to be used as pets (Carbone et al. 2003; Baumans et al. 2007). In addition, a study by Maligana et al. (2020) found that samples of *M. musculus* and *R. norvegicus* were affiliated to the laboratory strains. This warrants further investigation, which may include the sampling of both pet and laboratory rat and mice strains.

Mus musculus haplotype analysis revealed that most individuals belong to one highly abundant haplotype (NS106M) represented in all the provinces. Haplotype network for both separate and combined genes did not display a clear geographically correlated pattern. *CO1* and *Cyt-b* had higher genetic diversity than 16S RNA and CR, but singletons represented most haplotypes in these two genes. KwaZulu-Natal, Gauteng and North West Provinces had more unique haplotypes in all the gene regions, with some of the haplotypes being ancestral to unique haplotypes found in other provinces. Unique haplotypes indicate that there may have been several introductions of new strains showing that most pet shop owners acquire their pets from different sources, then supply them to other provinces. In addition, four unique haplotypes in Free State, Limpopo, Eastern Cape and Mpumalanga Provinces were closely related; therefore, they could have been sourced from Gauteng and North West Provinces. Our result also found a negative Tajima's D for *M. musculus* specimens, suggesting a steady population expansion.

For *R. norvegicus,* individuals belonged to two haplotypes not represented in all the provinces, and the results showed a subtle geographic structure. As a result, we suggest that further sampling will likely display shared haplotypes between the provinces. Even though few samples were analyzed, the haplotype analysis recovered eight haplotypes in the combined dataset and nine in the *Cyt-b* gene. The number of *Cyt-b* haplotypes in *R. norvegicus* samples was more than the number of haplotypes recovered in a study on wild populations of this species in South Africa (Bastos et al. 2011). More number of haplotypes in captive rodent populations could be because of the introduction of new strains in the pet trade industry. Genetic diversity is important as it enables the species to respond to threats such as predators, parasites, diseases and also environmental changes (Chen et al. 2012; Nguiffo et al. 2019). Consequently, if *M. musculus* and *R. norvegicus* haplotypes escape or intentionally released into the environment, they may be able to overcome such threats given that their haplotypes were genetically different. Although pet trade is not cited as an invasion pathway for *R.*

norvegicus in South Africa, rats with markings typical of laboratory and pet rat strains were observed living in feral conditions in Alexandra Township, South Africa (Maligana 2018). This suggests that there may have been several escapes and releases of these traded rodents in South Africa.

6.6 Conclusions

Our study revealed that rodent species sold in the South African pet shops have below-species genetic diversity. *Mus musculus* haplotype analysis did not show a clear geographical pattern, while *R. norvegicus* haplotype network showed a subtle geographic structure. As a result, we suggest further investigation with the addition of more *R. norvegicus* samples. Western Cape, Gauteng, North West and KwaZulu-Natal Provinces had more unique haplotypes not shared with any other provinces. In addition, our study concluded that *M. coucha* is not widely traded when compared with *M. musculus* and *R. norvegicus*. The introduction and breeding of these non-native species should be regulated because the continued introduction of species with high genetic diversity may influence their establishment, given that accidental escapes and intentional releases may occur. These results can be used when implementing management strategies regarding the trade of these species.

6.7 Acknowledgements

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6.8 Conflicts of interest/Competing interests

The authors declare no conflict of interest nor competing interests.

6.9 Authors' contributions

NS and SWM conceptualised and did the sample design. NS implemented the study. NS and TCS collected and prepared the samples. NS, TCS and SWM analysed the data. NS wrote the manuscript draft while TCS, SWM and CTD edited the manuscript.

6.10 Ethics approval

Not applicable

6.11 Data availability statement

Data for this study is available on request from the authors.

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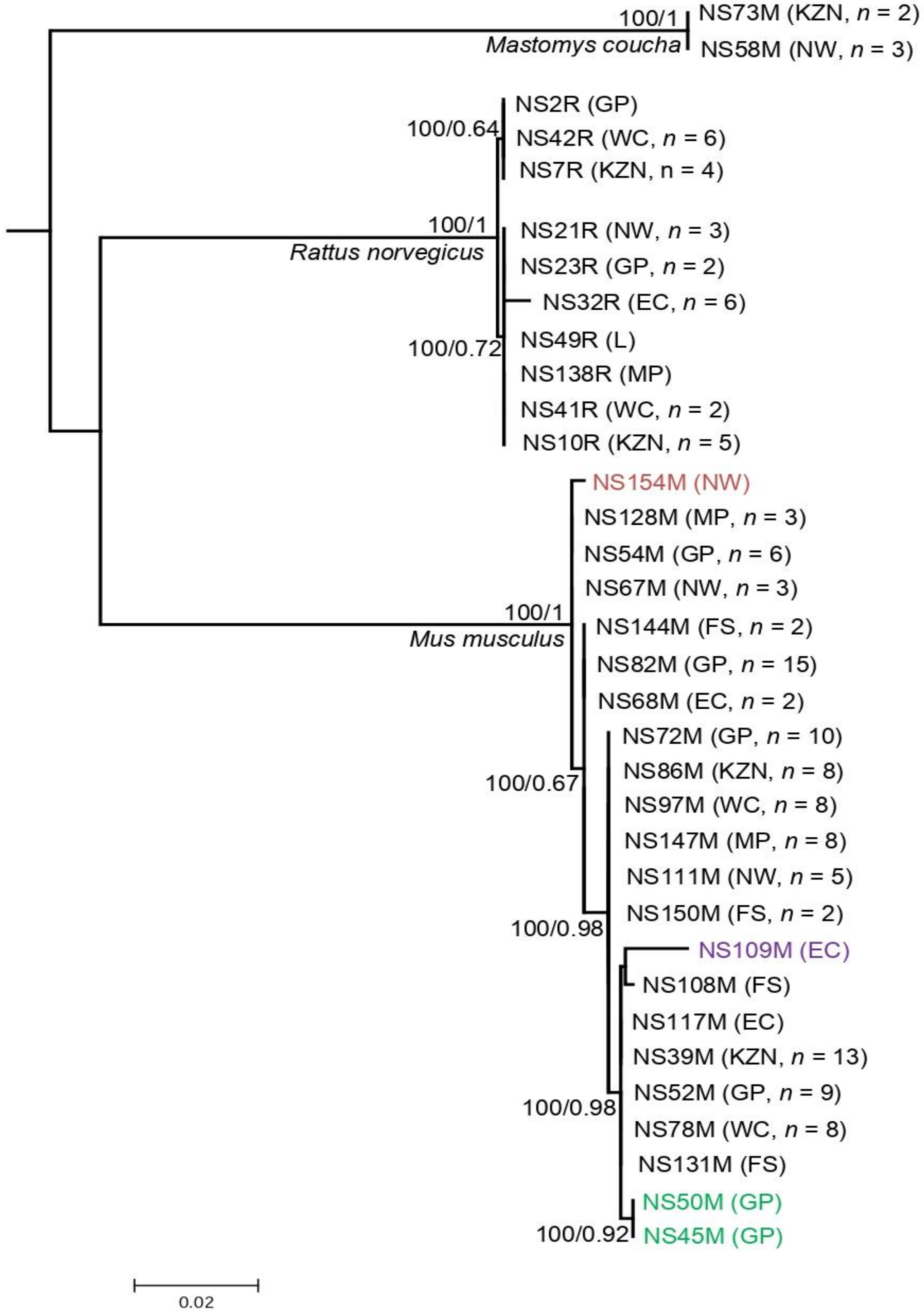
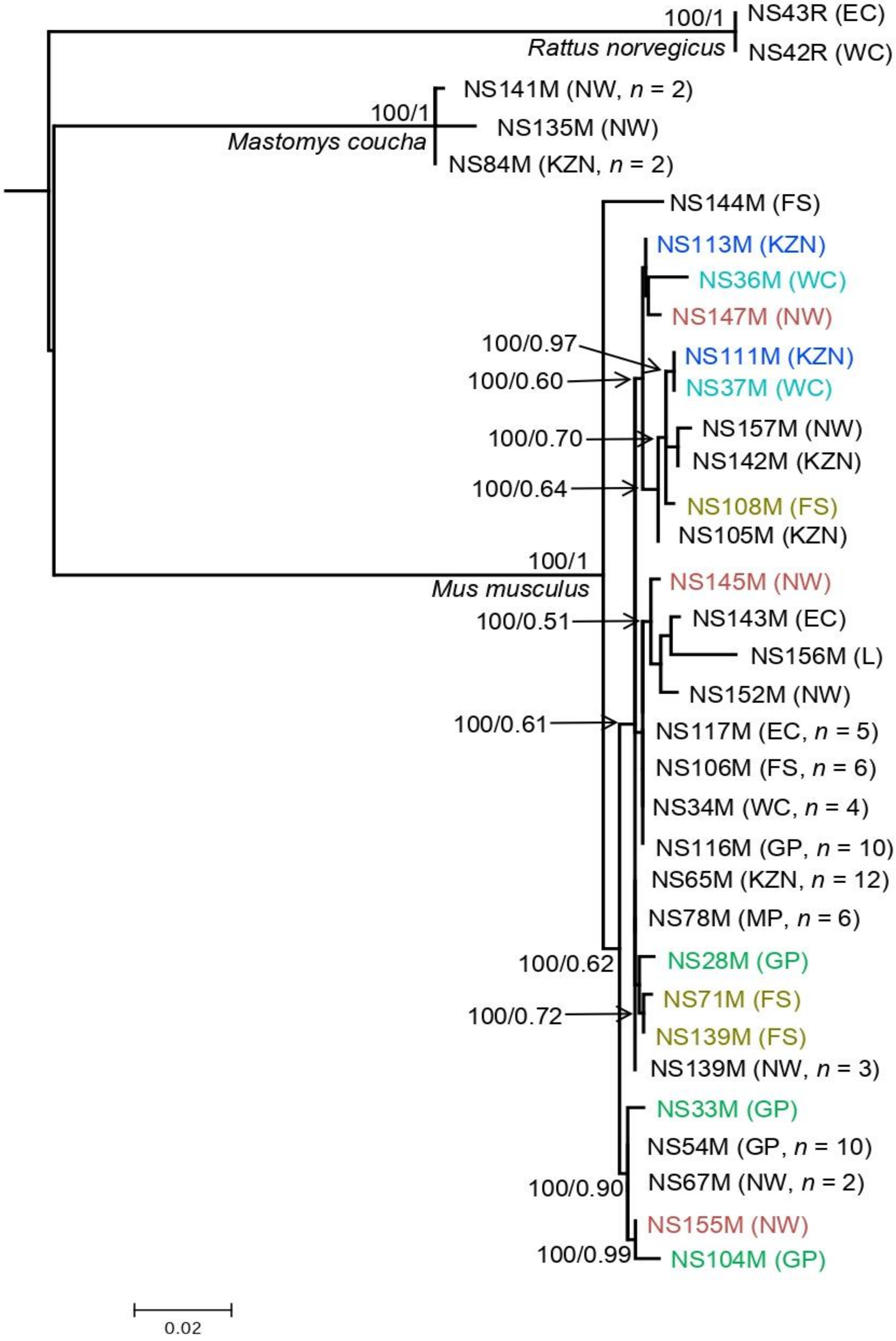
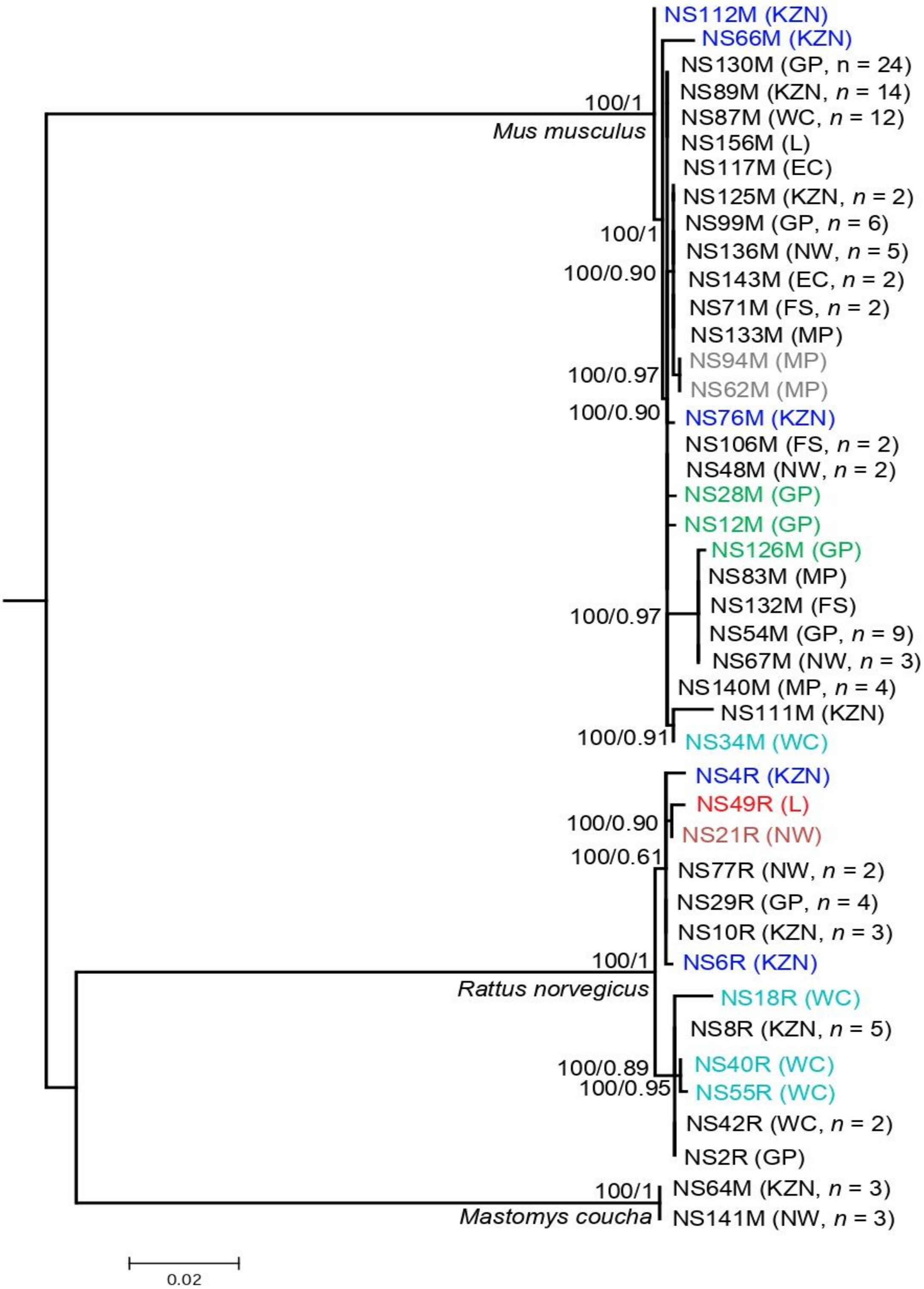
6.13 Supplementary Information



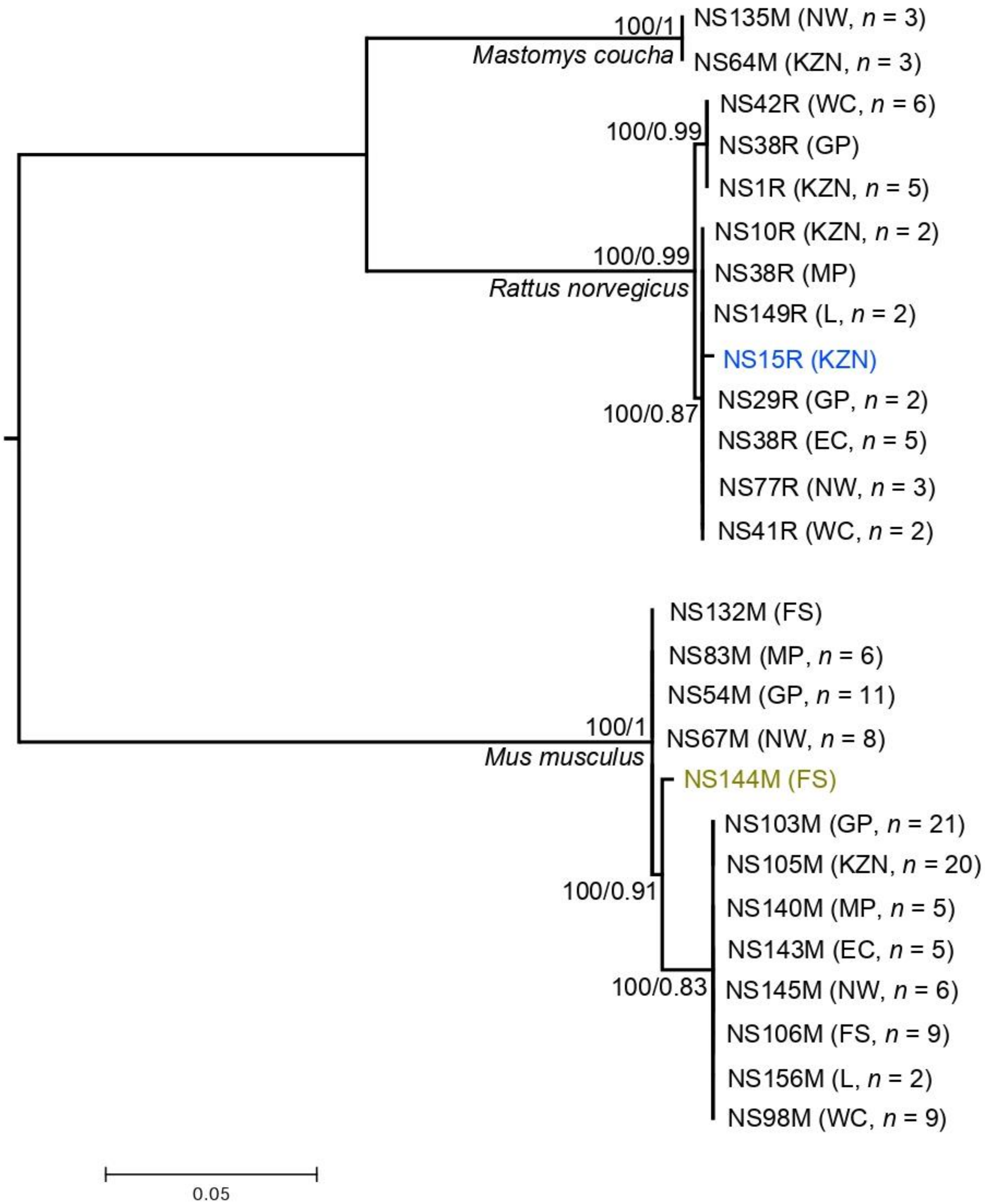
Supplementary Material Fig. S6.1 Most likelihood tree based on the analysis of 16S ribosomal RNA (16S rRNA) including *Mus musculus*, *Rattus norvegicus*, and *Mastomys coucha* collected from South African pet shops. Nodal support values represent maximum likelihood bootstrap (>50%) and Bayesian posterior probability (>0.6) support. The number of identical sequences is shown in parentheses, and the colour coded taxa show unique individuals. The provinces where samples were collected are abbreviated as follows: EC-Eastern Cape, FS-Free State, GP-Gauteng Province, KZN-KwaZulu-Natal, L-Limpopo, MP-Mpumalanga, NW-North West, and WC-Western Cape.



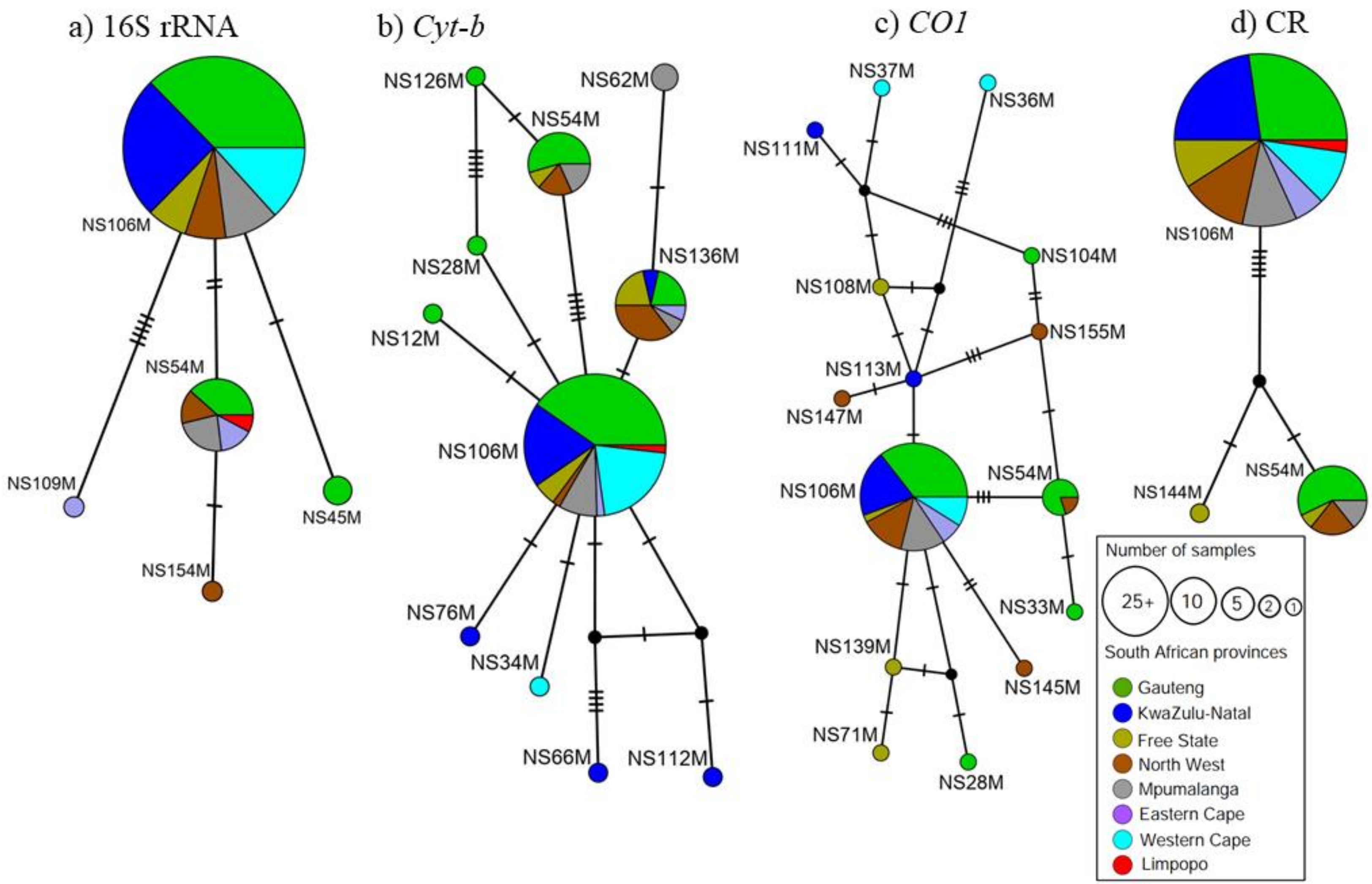
Supplementary Material Fig. S6.2 Most likelihood tree based on the analysis of *Mus musculus*, *Rattus norvegicus*, and *Mastomys coucha* based on mtDNA cytochrome oxidase subunit 1 (*CO1*) gene region. The individuals were collected from South African pet shops. Nodal support values represent maximum likelihood bootstrap (>50%) and Bayesian posterior probability (>0.6) support. The number of identical sequences is shown in parentheses, and the colour coded taxa show unique individuals. The provinces where samples were collected are abbreviated as follows: EC-Eastern Cape, FS-Free State, GP-Gauteng Province, KZN-KwaZulu-Natal, L-Limpopo, MP-Mpumalanga, NW-North West, and WC-Western Cape.



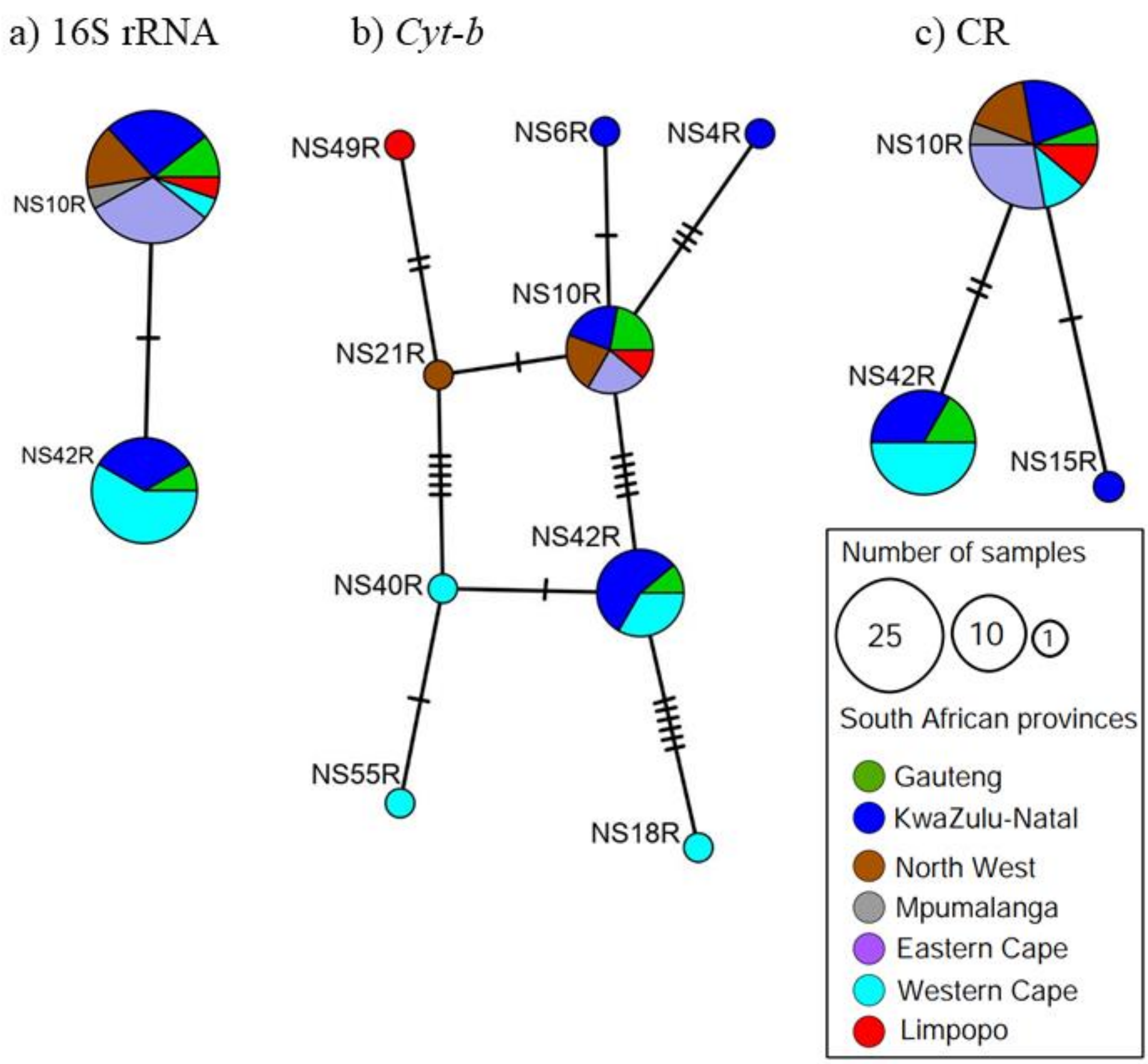
Supplementary Material Fig. S6.3 Most likelihood tree based on the analysis of *Mus musculus*, *Rattus norvegicus*, and *Mastomys coucha* based on mtDNA cytochrome b (*Cyt-b*) gene region. The individuals were collected from South African pet shops. Nodal support values represent maximum likelihood bootstrap (>50%) and Bayesian posterior probability (>0.6) support. The number of identical sequences is shown in parentheses, and the colour coded taxa show unique individuals. The provinces where samples were collected are abbreviated as follows: EC-Eastern Cape, FS-Free State, GP-Gauteng Province, KZN-KwaZulu-Natal, L-Limpopo, MP-Mpumalanga, NW-North West, and WC-Western Cape.



Supplementary Material Fig. S6.4 Most likelihood tree based on the analysis of *Mus musculus*, *Rattus norvegicus*, and *Mastomys coucha* based on mtDNA hypervariable control region (CR) gene region. The individuals were collected from South African pet shops. Nodal support values represent maximum likelihood bootstrap (>50%) and Bayesian posterior probability (>0.6) support. The number of identical sequences is shown in parentheses, and the colour coded taxa show unique haplotypes. The provinces where samples were collected are abbreviated as follows: EC-Eastern Cape, FS-Free State, GP-Gauteng Province, KZN-KwaZulu-Natal, L-Limpopo, MP-Mpumalanga, NW-North West, and WC-Western Cape.



Supplementary Material Fig. S6.5 Median-joining haplotype network constructed using data from four mtDNA gene regions (16S rRNA, *Cyt-b*, *CO1* and CR) based on sequences of *Mus musculus* sold in South African pet shops



Supplementary Material Fig. S6.6 Median-joining haplotype network constructed using data from four mtDNA gene regions (16S rRNA, *Cyt-b* and CR) based on sequences of *Rattus norvegicus* sold in South African pet shops

CHAPTER 7

General discussion and conclusions

7.1 Background

Pet trade is one of the major pathways through which non-native species are introduced to new environments (da Rosa et al. 2017; Lockwood et al. 2019; Maceda-Veiga et al. 2019). These pets are sold through various sources, including breeders, online (pet shops, social media and adverting websites), and physical pet shops (Maligana et al. 2020; Nelufule et al. 2020; Shivambu et al. 2020a). To date, the largest traded animal groups are reptiles, birds and the focus of this thesis, mammals (Mahmood et al. 2011; Bush et al. 2014; Green et al. 2020). Some non-native mammalian pet species have accidentally escaped or were intentionally released into the environment (Heinsohn 2004; Camarotti et al. 2015; da Rosa et al. 2017). Unfortunately, some of these mammalian pet species have established feral populations and become invasive, causing environmental and socio-economic impacts (Nogueira et al. 2011; Stojanovic et al. 2017; Shivambu et al. 2020b). Environmental impacts include preying on native species, hybridising with native species and competing with native species for food and space (Kumschick and Nentwig 2010; Nentwig et al. 2010). Socio-economic impacts include spreading zoonotic diseases to humans, negatively affecting the human infrastructure, animals, and agricultural production (Kumschick and Nentwig 2010; Nentwig et al. 2010). A total of 15 mammalian species have become invasive in South Africa through various pathways (Measey et al. 2020). Some of these invasive species are presented in the pet trade, although it is not the main pathway of their introduction (Shivambu et al. 2021). Given the above background, the following were investigated: 1) the extent of trade in non-native small mammals in South Africa, including which species are most popular, and the perception of pet shop owners (Chapter 2 and 3); 2) potential environmental and socio-economic impacts as well as their potential distribution (Chapters 4 and 5) and lastly, the taxonomy and genetic diversity of some rodent species in the South African pet shops (Chapter 6).

7.2 Main findings and discussion

7.2.1 Non-native small mammal pets in South Africa

In South Africa, the trade of non-native pets is growing, and some of the traded small mammals are regarded as invasive species in the country and its off-shore islands (Measey et al. 2020). A total of 122 pet shops and seven online sources selling 24 and 16 non-native species, respectively, in South Africa were found (Chapter 2). As predicted, the species richness in pet shops was lower than in online trade. This could be explained by that pet shops are strictly regulated as opposed to online trade, which is difficult to trace (Haas and Ferreira 2015; Pasmans et al. 2017). The most popular species in both sources of trade were the Norwegian rat *Rattus norvegicus*, house mouse *Mus musculus*, Guinea pig *Cavia porcellus*, and the European rabbit *Oryctolagus cuniculus* (Chapter 2). The most common species were predicted to be cheaper when compared with the least popular species. *Rattus norvegicus* and *M. musculus* were traded from as little as ZAR 9.00 (0,60 USD) per species (Chapter 2). Price has been indicated as one of the important factors to determine the release and escape events (Vall-llosera and Cassey 2017; Shivambu et al. 2020a; Nelufule et al. 2020), given that the amount of care given to a species is related to its value. This study found that species sold in large numbers, listed as Appendix I under CITES, non-CITES, least concern, vulnerable to extinction, not known to be invasive and invasive in South Africa, were sold at relatively lower prices (Chapter 2). In this case, rodents and the *O. cuniculus* poses a high risk of becoming invasive in South Africa, given that they were popular, sold at low prices and most of them are not protected for trade by CITES (Chapter 2). Some primate species are not likely to become invasive in South Africa, as they are traded at low volume, most expensive and protected for trade by CITES (Chapter 2). The trade in non-native species is influenced by an ever-increasing population and economic status of the countries (Shepherd et al. 2007; Shivambu et al. 2021). Three provinces, Gauteng, KwaZulu-Natal and Western Cape, were found to have more physical pet shops, online sales, high species richness and abundance (Chapter 2). This could be explained by these provinces having a high human population, and their GDP is high compared with other provinces of South Africa (STATS SA 2019).

7.2.2 Pet shop owners' perceptions

Most countries have laws that regulate the trade of non-native species. Despite this, the trade of these species continues, and it includes species on CITES (Siriwat and Nijman 2018; Maceda-Veiga et al. 2019). In South Africa, the trade of species is regulated by the National Environmental Management Biodiversity Act (NEM:BA). This act prohibits the sale of some non-native small mammals; for example, *M. musculus*, *O. cuniculus* and *R. norvegicus* are prohibited from sale on the off-shore islands and not on the mainland (DEA 2016). To get an overview of the knowledge of the law, sources of trade and species sold, a total of 122 pet shop owners/ managers in South Africa were surveyed (Chapter 3). It was predicted that rodents would be the most popular species traded than other taxa. As predicted, most pet shop owners sell *R. norvegicus, M. musculus, C. porcellus*, and *O. cuniculus* (Chapter 3). The increased sale of these species could be because they are also sold as feeders for other animals, such as snakes, tarantulas and amphibians (Cooper and William 2014; Kanagarajah et al. 2018; Rawski et al. 2018). It was also predicted that pet shop owners acquire their pets from different sources. The most common source of the trade from where these species were obtained included breeders, animal rescues, and pet shops (Chapter 3). This indicated that breeders may be supplying most of the traders in South Africa, and pet shop owners may be exchanging some pets as pet shop was indicated as the third-largest source from where the respondents obtain their pets. Most respondents were aware of NEM:BA regulations (Chapter 3). This may indicate that most of the small mammalian species sold by pet shop owners are legal. However, legally sold pets poses an invasion risk given that pet shop owners do not track whom they are selling the species to. This could also be because the general public may not be aware of the species being sold or the legislation especially if the pet shop owners responsible for selling the species do not know the trading regulations (Chapter 3).

7.2.3 Potential impacts of non-native small mammal pets

To understand which non-native small mammal pets may potentially cause environmental and socio-economic impact, the Generic Impact Scoring System was used (Chapter 4). Of the 24 species, impacts results were obtained for only ten species (Chapter 4). It was predicted that most of the non-native small mammalian species traded as pets in South Africa would be more associated with socio-economic impacts rather than environmental impacts. However, it was found that there were no significant differences between overall environmental and socio-economic impact scores, although the latter had a higher overall impact score (Chapter 4). For socio-economic category, non-native small mammalian species represented potential impacts on agricultural and animal production (livestock), while for the environmental impact category, the impacts on animals (predation), competition and hybridisation prevailed (Chapter 4). *Oryctolagus cuniculus* displayed the highest potential to cause both environmental and socio-economic impacts, given that it had the overall high impact score (Chapter 4). Rodent species such as *M. musculus* and *R. norvegicus* also scored high in both environmental and socio-economic impacts (Chapter 4). These two species may be causing some of the impacts reported for other countries in South Africa, given that they are regarded as invasive species in the country (Measey et al. 2020). In addition, *R. norvegicus* may be threatening the health of humans in the urban landscapes, given that they have been found to carry zoonotic agents such as helminths, toxoplasmosis and leptospirosis (Taylor et al. 2008; Julius et al. 2018).

7.2.4 Species distribution modelling and human footprint to predict potential suitability

To further understand which non-native mammalian species may potentially establish feral populations, the species distribution modelling and human footprint for commensal species were used (Chapter 5). A total of 14 species that met the selection criterion (Chapter 5) were evaluated. The results showed that species with high availability in the pet trade and extensive occurrence records tended to have larger climatic suitability when compared with non-invasive species with low trade volumes (Chapter 5). In addition, the distribution records of the species already invasive in South Africa, *M. musculus* and eastern grey squirrel *Sciurus carolinensis* overlapped with the predicted suitability (Chapter 5). However, for *R. norvegicus*, some of the distrubtion records in South Africa did not overlap with the predicted suitability, e.g. in Gauteng and Limpopo Provinces. This suggests that these species would expand their distributions in South Africa if the climate plays a role in their invasion success. In addition, *R. norvegicus* would potentially have larger distributions given that the human footprint contributed to its potential distribution in South Africa (Chapter 5). Humans are likely to move this species to highly suitable areas where it is not yet recorded through the pet trade. Most of the species' present selling points fell within the predicted suitability, suggesting that the trade for those species should be monitored (Chapter 5).

7.2.5 Molecular analyses to identify mammalian species in the pet trade

To successfully monitor the trade, species inventories based on molecular analyses are important since some of the species are incorrectly identified in the pet trade industry (Maligana et al. 2020; Nelufule et al. 2020; Shivambu et al. 2020). Knowing the correct identity of a species also assists in accessing its actual distribution in the pet trade industry (Strecker et al. 2011; Ng et al. 2016). In addition, molecular analyses are useful in determining the source of origin of the traded species and evaluating the rate of successful invasions (Collins et al. 2002; Campbell et al. 2019). Pet trade is responsible for the introduction of several non-native small mammalian species (Gippet and Bertelsmeier 2021), and with the desire to breed or introduce new or rare varieties, genetically varied source populations may be released or escape captivity and establish feral populations. Molecular analyses based on four mitochondrial gene data were used to identify and assess the genetic diversity of rodent species sold in the South African pet shops (Chapter 6). The geographic distribution pattern of rodent species genetic diversity was also investigated. It was predicted that there is genetic diversity within the rodent species sold in South African pet shops, and they follow a clear geographically correlated pattern. The phylogenies for both the separate and combined datasets revealed three distinct clusters belonging to *M. musculus*, *R. norvegicus* and *M. coucha*. *Mus musculus* and *R. norvegicus* had several strains and were traded in different provinces compared with *M. coucha*, which was found in two provinces (Chapter 6). This may indicate that native small mammals are not widely traded when compared with non-native species in South Africa and that there is compliance in terms of the trading regulations for native species (DEA 2016; Chapter 6).

A total of 19 unique haplotypes were identified for *M. musculus*, while *R. norvegicus* had eight haplotypes (Chapter 6). *Mus musculus* combined dataset recovered a starburst haplotype network, indicating that there were no clear geographically correlated genetic diversity patterns (Chapter 6). However, *R. norvegicus* did show some very subtle geographic structure, with KwaZulu-Natal, North West, Gauteng, and Eastern Cape Provinces indicated as the sources of breeding populations for other haplotypes (Chapter 6). According to the haplotype network for both species, it is suggested that specimens that had the same haplotype originated from the same source population, while individuals with unique haplotypes originated from different populations (Chapter 6). Although pet trade is an uncommon pathway of invasion for these rodent species, rats with markings typical of laboratory and pet rat were observed living in feral conditions in Alexandra Township, South Africa (Maligana 2018). The role of the pet trade in the establishment of non-native small mammalian species with greater genetic diversity needs further investigation. In this case, *M. musculus* and *R. norvegicus* may be good study species to test this hypothesis given that they are popular in the pet trade, small, can be easily collected in the pet shops as they are also sold frozen and are already invasive in South Africa.

7.3 Conclusions and recommendations

The trade of non-native small mammalian species is relatively large in South Africa and this trade represents some of the highest potential invasive species with the risk of causing environmental and socio-economic impacts. As a result, it is recommended that the public health institutions, pet trade industry, researchers, pet owners, and policy developers engage in discussions that include thorough monitoring of the pet trade industry, modifying existing pet trade regulations, and educating the general public about the potential impacts with non-native pets. It is also proposed to include invasive species that are already invasive in South Africa in the current legislation, as they were found with high potential impacts and invasion risk. This can be achieved by engagements with the pet trade industry, researchers, policy-makers, animal rescuers and veterinarians. Such engagements are lacking as there are some pet shop owners who have no knowledge of the current laws regulating the trade. CITES-listed species, including endangered primates, are traded in South Africa, and this may need government interventions as these species are offered at higher prices. As a result of their price, they may be overexploited in their native ranges to meet the trade demand. There are undoubtedly other species of small mammals that were not recorded in the current study. Therefore, continued monitoring of the trade is recommended to maintain a complete inventory of all the species imported into the country. Areas with selling points within the predicted suitability should be monitored, and active surveillance in those areas is recommended so that released or escaped species could be detected before they start to spread and become invasive.

7.4 Future work

This study has provided an insight into the trade of non-native small mammalian species in South Africa and their potential impacts. Despite this, a lot more still needs to be done in future studies:

1) This study only investigated the trade in two sources of trade (online and physical pet shops). As a result, future studies should monitor the introduction of these species through breeding facilities since it was the main source from where pet shops acquired their pets.
2) The survey questionnaire revealed that some pet shop owners were not aware of the NEM: BA regulation. Since this study did not investigate if the pet shops were complying with the regulations, future studies should determine if the trade regulations in various provinces are adhered to.
3) Pet shop owners indicated that they also sell other animal taxa. It is, therefore, suggested that a thorough investigation should be conducted for other taxa sold, so that an inventory of taxa not previously studied in the pet trade is collated.
4) Wild is another source of the trade from where pet traders acquire their pets. However, it has been indicated that wild-caught animals are illegal to sell, and only captive-bred animals are legal for sale (Bulte and Damania 2005; Campbell et al. 2019). Currently, it is not known if South African species imported for trade are illegally harvested from

the wild. Therefore, it is recommend that future studies determine the source of origin of the traded species using molecular analyses (see Campbell et al. 2019).

7.5 References

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