

Chapter 5

Terrestrial Vertebrate Invasions in South Africa



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Abstract In this chapter we review the current knowledge on terrestrial vertebrate invasions in South Africa. Thirty species of mammals, birds, reptiles and amphibians are considered to have arrived over the last 10,000 years, with two thirds having become invasive in the last 150 years. Half of the species are mammals, a third birds, with three reptiles and two amphibians. Although there are multiple pathways, there appears to be a trend from species that were deliberately introduced in the past, to accidental introductions in the last ~100 years, which are a by-product of increasing trade, both internationally and within South Africa. Few invasive terrestrial vertebrate species have had their impacts formally assessed within South Africa, but international assessments suggest that many can have Moderate or Major environmental and socio-economic impacts. Of particular concern is the growing demand for alien pets within the region, with increasing amounts of escapees being encountered in the wild. We consider the importance that the NEM: BA Alien and Invasive Species Regulations have had on the research of invasive terrestrial vertebrates in South Africa, and emphasise the importance of regulations for domestic exotics.

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5.1 Introduction

The emphasis on biological invasions in South Africa (as elsewhere in the world) has historically been on plants, because of their visibility, their perceived higher impact and the large areas they have invaded in different biomes of the country (Pyšek et al. 2008; Richardson and van Wilgen 2004). Animal invasions have received notably less attention, and only following the passing of South Africa's National Environmental Management: Biodiversity Act (Act No. 10 of 2004) (hereafter NEM:BA) were legal and financial measures put in place to control or remove them. Vertebrate invasions in freshwater environments (i.e. all fishes) are covered elsewhere in this book (Weyl et al. 2020; Chap. 6). In this chapter we provide information on 30 invasions by vertebrate species (mammals, birds, reptiles and amphibians, Table 5.1).

Many of South Africa's invasive vertebrates have undergone rapid range expansions, or been transported within the region, beyond their historical ranges. These are often referred to as extralimital (e.g. Spear and Chown 2009a), or even as domestic exotics (Guo and Ricklefs 2010), and therefore many have not been historically included in lists of invasive species, as they are not alien to the geopolitical unit of South Africa. Our selection of species included here was initially based on terrestrial vertebrate invasions listed in Picker and Griffiths (2017), but we have augmented this to include other vertebrate species that fit the definition of "alien" by Richardson et al. (2011a). We acknowledge that there are many alien vertebrates present in captivity (stages B1, B2, B3 in Blackburn et al. 2011), and that there are also individuals that have been released from captivity both intentionally and accidentally, or transported out of their natural range (stages C1, C2). These species may become important emerging invaders, and we refer to them explicitly in passing. In this chapter species accounts are provided for those that have formed self-sustaining populations, including all stages up to full invasions (stages C3, D1, D2, E).

5.2 History of Introductions, Pathways and Vectors

Prior to the arrival of European ships, South Africa was inhabited by peoples already using domestic animals, such as Sheep, *Ovis aries*, Cattle, *Bos taurus*, Goats, *Capra hircus* and Dogs *Canis familiaris* that were all alien to the region (see Faulkner et al. 2020, Sect. 12.2.2.1). Ships sailing around the coast at this time likely brought with them early invaders, such as rats and mice. Although records are missing for this period, credence to this scenario comes from the knowledge that rats (and presumably mice, although the two were both referred to as rats historically) were present in large numbers prior to the arrival of European settlers (Crawford and Dyer 2000), and genetic studies on rats suggest movements from the Indian subcontinent were concurrent with those to East Africa (Aplin et al. 2011).

Table 5.1 Terrestrial vertebrate invasions treated in this chapter, and sorted by expected chronological appearance as invasive species in South Africa

Group	Species name	Common name	Origin	Year	Pathway	Intentional/unintentional/ accidental
Mammal	<i>Mus musculus</i>	House mouse	Eurasia	~800	Stowaway (bulk)	u
Mammal	<i>Rattus rattus</i>	House rat	South Asia	~800	Stowaway (bulk)	u
Mammal	<i>Capra hircus</i>	Goat	Iran	1650	Escape (farmed animals)	i
Mammal	<i>Equus asinus</i>	Donkey	Egypt Somalia	1650	Escape (farmed animals)	i
Mammal	<i>Equus ferus caballus</i>	Horse	Central Asia	1650	Escape (farmed animals)	i
Mammal	<i>Felis catus</i>	Domestic cat	Egypt	1650	Escape (pet)	i
Mammal	<i>Rattus norvegicus</i>	Brown rat	China, Russia, Japan	1650	Stowaway (bulk)	u
Mammal	<i>Oryctolagus cuniculus</i>	European rabbit	Europe	1654	Escape (farmed animals)	i
Bird	<i>Columba livia</i>	Rock Dove	Mediterranean Asia	1850	Escape (pet/farmed animal), Release (hunting)	i
Mammal	<i>Dama dama</i>	Fallow Deer	Iran Iraq Turkey	1869	Escape (ornamental)	i
Mammal	<i>Rusa unicolor</i>	Sambar Deer	South East Asia	1880	Release (hunting)	i
Bird	<i>Sturnus tristis</i>	Common Myna	South Asia	1888	Escape (pet)	i
Bird	<i>Sturnus vulgaris</i>	Common Starling	Europe	1889	Escape (ornamental)	i
Bird	<i>Fringilla coelebs</i>	Chaffinch	Europe	1890	Escape (ornamental)	i
Mammal	<i>Sciurus carolinensis</i>	Grey squirrel	USA	1890	Escape (ornamental)	i
Bird	<i>Passer domesticus</i>	House Sparrow	Eurasia Northern Africa/India	1893	Escape (pet)	u
Reptile	<i>Ramphotylops braminus</i>	Flowerpot Snake	South Asia	1920	Contaminant (nursery materials)	u
Mammal	<i>Sus scrofa</i>	Domestic Pig	Eurasia	1926	Release (biocontrol, hunting)	i
Mammal	<i>Hemiragrus jemtahicus</i>	Himalayan Tahr	Central Asia to China	1930	Escape (ornamental)	u
Bird	<i>Anas platyrhynchos</i>	Mallard	Nearctic	1940	Escape (ornamental/pet), Release (hunting)	i
Reptile	<i>Lygodactylus capensis</i>	Common Dwarf Gecko	Central Africa	1956	Contaminant (transportation of habitat material)	u

(continued)

Table 5.1 (continued)

Group	Species name	Common name	Origin	Year	Pathway	Intentional/unintentional/ accidental
Bird	<i>Alectoris chukar</i>	Chukar Partridge	Central Asia	1964	Escape (ornamental)	i
Bird	<i>Psittacula krameri</i>	Rose-ringed Parakeet	South Asia	1970	Escape (pet)	u
Bird	<i>Corvus splendens</i>	House Crow	South Asia	1972	Stowaway (container)	i
Bird	<i>Pavo cristatus</i>	Peafowl	South Asia	1975	Escape (ornamental)	u
Mammal	<i>Hippotragus equinus koba</i>	Western Roan	West Africa	1980	Release (hunting)	i
Reptile	<i>Hemidactylus mabouia</i>	Tropical House Gecko	Central Africa	1980	Contaminant (transportation of habitat material)	u
Amphibian	<i>Hyperolius marmoratus</i>	Painted Reed Frog	Central Africa	1995	Contaminant (nursery materials), Stowaway (vehicles)	u
Amphibian	<i>Sclerophrys gutturalis</i>	Guttural Toad	Central Africa	1998	Contaminant (transportation of habitat material)	u
Mammal	<i>Rattus tanezumi</i>	Tanezumi Rat	Asia	2005	Stowaway (bulk)	u

The original table follows that of Pickett and Griffiths (2017), with additional taxa that meet the definition of invasive. Pathways are from van Rensburg et al. (2011), according to Harrower et al. (2017)

The Cape (currently Western Cape and Eastern Cape provinces) then became a significant staging post for shipping traffic between Europe and Asia from 1600 to the 1850s. European settlers brought with them more pests and many domestic animals, some of which were deliberately let loose to breed for the purposes of supplying meat. These early pathways by ship were dominated by deliberate introductions. Notable among them were the efforts by the Dutch colonial administrator, Jan van Riebeeck, to establish a colony of rabbits on Robben Island, which he reported in his journals in the mid-1600s.

By the mid-1800s societies formed in many colonies to deliberately introduce species that reminded them of their European origins. In South Africa, many such introductions are attributed to British businessman, mining magnet and politician Cecil John Rhodes, Prime Minister of Cape Colony 1890–1896, who is said to have introduced *Sturnus vulgaris* (Common Starling), and *Fringilla coelebs* (Common Chaffinch), as well as *Dama dama* (Fallow Deer), and *Sciurus carolinensis* (Grey Squirrels), which were themselves introduced to England from North America (Brooke et al. 1986). During this time there were many more introductions of species that failed to establish, records of these include four more birds introduced by Rhodes: *Corvus frugilegus* (Rooks) *Luscinia megarhynchos* (Nightingales), *Turdus merula*, (Blackbirds) and *T. philomelos* (Song Thrushes).

The most recent period, over the last 100 years, is associated with the advent of increased trade between South Africa and broader global markets, the growth of the game-farming industry, an expansion of the protected area network and subsequently ecotourism. The continued growth in trade both externally and within South Africa (Faulkner et al. 2017) has resulted in a dramatic rise in accidental introductions, including reptiles and amphibians, as well as more birds and mammals. Deliberate introductions, however, persist.

The game industry has emerged as a significant pathway for the introduction of large herbivorous mammals. The importance of the game industry in South Africa has resulted in 38 ungulate species being introduced, which is globally second only to the USA (70 species Spear and Chown 2009a). A countrywide survey found that of 47 large herbivores present in large commercial tourism or game ranching operations, 10 were alien and 15 extralimital (Castley et al. 2001). Moreover, all operations surveyed stocked at least one of these alien mammal species. The mixing of native and extralimital species in South Africa has provided a particular problem as this has often resulted in hybridisation, threatening the genetic integrity of native stocks (Spear and Chown 2008, 2009a, b).

There are a large number of alien mammal species in South Africa (42 reported by van Wilgen and Wilson 2018 and 51 by van Rensburg et al. 2011), but only a few (15) of these are invasive or established.

Currently, invasive reptiles in South Africa have all arrived as accidentally-transported contaminants of the horticultural trade, within consignments of firewood, and in building materials. However, there is a global trend for the importing and keeping of alien pets, especially reptiles (Herrel and van der Meijden 2014; Schlaepfer et al. 2005), and a result is the subsequent release of a proportion of these animals into the wild (Stringham and Lockwood 2018). In South Africa, there are

numerous reports of encounters with escaped or released pet reptiles. To date, pet reptiles are not known to have become established in the country, but there has been an exponential increase in imports from an increasing number of originating countries (van Wilgen et al. 2010). However, nearly 300 species of alien herpetofauna are known to have been imported into South Africa and are in captivity (van Wilgen et al. 2008). South Africans have a preference for pet reptiles that are large, easy to breed and colourful (van Wilgen et al. 2010).

Like reptiles, amphibian invasions in South Africa are currently minimal, but there is concern that increases in trade may bring about new invasions (Measey et al. 2017; van Wilgen et al. 2008; Measey et al. 2019; Mohanty and Measey 2019). Incidents of jump dispersal as contaminants of horticulture, with wood and even adhered to vehicles are apparently common, likely underreported, and include international as well as local movements (Measey et al. 2017). Suggestions have been made that certain taxonomic groups of southern African amphibians are predisposed to being moved large distances, such that they pose a threat to countries outside the region. Of particular note in this respect are the ongoing invasions of *Sclerophrys gutturalis* (Guttural Toad) and *Hyperolius marmoratus* (Painted Reed Frog). A common feature of South African invasive amphibians is the use of novel permanent man-made water bodies, in the form of farm impoundments or garden ponds, as a resource that facilitates reproduction and dispersal through stepping-stone movement across the landscape (Davies et al. 2013; Measey et al. 2017).

Xenopus laevis (the African Clawed Frog) is endemic to South Africa, but invasive on four other continents (Measey et al. 2012). Genetic investigations of many of the invasions show the source population to be the extreme south-east of the country (e.g. De Busschere et al. 2016; Wang et al. 2019), following the evangelical breeding and distribution of species by nature conservation authorities (see van Wilgen 2020, Sect. 2.1, and Weyl et al. Chap. 6). African clawed frogs were exported for pregnancy testing of people, and later for scientific investigations, but most recently as pets (Gurdon and Hopwood 2003; van Sittert and Measey 2016), but most animals imported into the USA were bred in China, with no ongoing trade from South Africa (Measey 2017). In South Africa, the African clawed frog has undoubtedly extended its range by utilising artificial impoundments, as well as being seeded by fishermen for later use as bait (Measey et al. 2017).

5.3 Mammalia

5.3.1 *Sus scrofa* (Domestic Pig)

Domestic Pigs were originally introduced to South Africa by Neolithic farmers around 9000 years ago (Picker and Griffiths 2011). Since this time, *S. scrofa* is likely to have formed part of the manifest of many shipping vessels, and additional stocks arrived to populate farms. Deliberate attempts to establish self-sustaining feral populations were also made by the Department of Forestry as a form of biological

control against the effects of the larvae of the sphingid moth *Nudaurelia cytherea* (Emperor Pine Moth) in pine plantations of Tulbach (1926) and Franschhoek (1941) (Picker and Griffiths 2011; Skead et al. 2011). There were also likely to be small populations of feral pigs that escaped from domestic stock throughout the country. Of particular note is the growth in demand for free-range pork and bacon that is thought to have resulted in sharp increases in established populations in the Western Cape (R. van der Walt pers. comm). Feral populations of *S. scrofa* were assessed as having Massive environmental impact, and Moderate socio-economic impact, with the highest summed scores for impacts of any of the mammals assessed by Hagen and Kumschick (2018). In South Africa, the socio-economic damage reported is thought to be relatively minor (Spear and Chown 2009a), although concern has been raised about their impacts on the threatened *Psammobates geometricus* (Geometric Tortoise) and some rare geophytes, prompting a control programme in Porseleinberg and Kasteelberg. To date, 1209 feral pigs have been removed, with the population from Kasteelberg coming close to extirpation (van Wilgen and Wilson 2018). In terms of the NEM:BA Alien and Invasive Species Regulations (hereafter “the Regulations”), the species is listed in context of specific sites.

5.3.2 *Felis catus* (Domestic Cat)

Domestic Cats have been introduced around the world, and are one of the highest impact invasive vertebrate predators (Hagen and Kumschick 2018). Their introduction to South Africa probably coincided with early ships and the rodents that came with them (see below). Some authors distinguish between feral cats, strays and domestic cats (Dickman 2009), but here we treat them together, as they are often in continuum and their impacts on the environment appear similar. While the impact of cats is undoubtedly highest on island fauna (Chap. 8, Greve et al. 2020; Courchamp et al. 1999), they have also resulted in the extinction of continental land birds (Dickman 2009). Estimates of predation rates have varied greatly and mostly consist of prey carried to the owners’ homes. But video cameras fitted to collars suggest that cats each kill 2–5 small animals per week, with only a quarter of prey items taken home, half of prey items are left in the field and the remainder eaten (Loyd et al. 2013). The density of cats in urban areas is estimated to be typically around 400 cats/km² (in the UK, Sims et al. 2008). Densities of cats in Cape Town have been estimated as 80–300 cats/km², and are thought to be lower due to the existence of numerous small carnivores (Caracal, *Caracal caracal*, mongooses, and some birds of prey) which are thought to control their numbers (F Morling unpublished data; George 2010; Peters 2011). In a South African urban conservancy (in KwaZulu-Natal) the density of cats was found to be between 23 and 40 cats/km², with densities likely augmented by supplemental feeding (Tennent and Downs 2008). Despite regular meals for most cats in Cape Town’s suburbs (estimated density of cats 150 cats/km²), their kill rates estimated using kitty cams, suggest that annual kills might be as high as 26 million animals, composed of 42% small

mammals, 30% invertebrates, 12% reptiles, 9% amphibians and 7% birds: alien prey items were less than 10% of the total (F Morling unpublished data). Individuals have a home range of around 30 ha, with animals moving up to 0.85 km in a straight line (George 2010).

In addition to predation, cats may have a substantial sub-lethal or indirect effect on avifauna, or facilitate invasion meltdown from third-party predators, such as corvids (Bonnington et al. 2013). High densities of these predators around the nesting sites of birds are thought to reduce provisioning to nestlings and result in reduced fitness. Cats continue to be stocked in many areas as they are perceived as effectively controlling invasive rodent populations (see below). For example, cats (together with domestic dogs, *Canis lupus familiaris*) create a landscape of fear in rural southern African homesteads, changing the foraging patterns of house rats and other pest rodents (Themb'alilahlwa et al. 2017). Other impacts in South Africa include the potential for hybridisation with African wildcats, *Felis silvestris lybica*. In a genetic study, le Roux et al. (2015) found evidence of hybridisation linked with a human population pressure gradient, with pure wildcats in the Kgalagadi Transfrontier Park, while samples from around Kruger National Park demonstrated some introgression. Despite their clear MR impacts (Hagen and Kumschick 2018), control of cats has the potential to cause conflicts thought to include aesthetic and moral values (Zengeya et al. 2017), hence they are only recognised in the Regulations in specific contexts (on South Africa's offshore islands: see Chap. 8, Greve et al. 2020).

5.3.3 *Equus asinus* (Donkeys)

Donkeys derive from native African wild asses, *Equus africanus*, which are still extant in Eritrea and Ethiopia (Moehlman et al. 2015). They, however, arrived in South Africa via shipping with Europeans in the 1600s (Blench 2004). Little is known about the extent and impact of feral donkeys in South Africa, although it was suggested the greatest threat they pose in this region is hybridising with Cape Mountain Zebra, *Equus zebra zebra* (Brooke et al. 1986; Fig. 5.1), producing a 'zonkey'. They are used by various communities and farmers as working animals, but are often neglected and allowed to roam free, causing competition between donkeys and other livestock, such as goats and sheep (Cupido and Samuels 2009; Samuels et al. 2016). A large feral donkey problem was reported from Paulshoek in the Karoo, where residents complained that donkeys were destructive towards vegetation (Hoffman et al. 1999). Recent aerial counts around Steinkopf and Leliefontein estimate that there are as many as 274 donkeys in this area, potentially consuming ~8% of the grazing available for productive livestock (Muller and Bourne 2018). Although there are no data to show the effect of donkeys on the environment in South Africa, they lead to local degradation of the environment, as occurs in Australia. In Australia, there are an estimated 5 million feral donkeys (Roots 2007) which are regarded as an invasive pest and have negative impacts on



Fig. 5.1 A hybrid between a Cape Mountain Zebra (*Equus zebra*) and a donkey (*Equus asinus*) near Cape Infanta in the Western Cape Province. Photograph courtesy of Brian van Wilgen

the environment. In their assessment, Hagen and Kumschick (2018) found that donkeys can have Massive environmental impact, but only Moderate socio-economic impact. They compete with livestock and native animals for food and space, spread invasive plants and diseases, foul or damage waterholes and cause erosion (Australian Government 2011). In South Africa, local abundance has led to export of donkey skins from communal areas for the traditional Chinese medicine and cosmetics market (Cruise 2018). As this often appears to be unregulated, there is also a growing animal welfare concern for these donkeys (Cruise 2018). They are not listed as invasive alien species in the Regulations.

5.3.4 *Equus ferus caballus* (Domestic Horses)

Horses arrived in South Africa via shipping with European settlers in the 1600s. They were used extensively for transport in South Africa before the introduction of automobiles. Since then they have been used on farms and for recreation. In rural communities they are still used for transport, but this is decreasing (Swart 2010). Little is known about the extent and impact of feral horses in South Africa, with nothing found on impacts in the formal peer-reviewed literature. There are three known wild horse populations in South Africa. Two are local tourist attractions. The largest is a population of at least 200 around Kaapsehoop in Mpumalanga, which roam an area of about 17,000 ha. The Kaapsehoop area is home to one of the last

Blue Swallow, *Hirundo atrocaerulea*, populations, and as livestock trampling has been shown to negatively affect Burrowing Owls, *Athene cunicularia* elsewhere (Holmes et al. 2003), the horses may be similarly affecting the burrow-nesting swallows. Another population is in Rooisands Nature Reserve and surrounding properties near Kleinmond in the Western Cape. No data are available in the formal literature on either population. Muller and Bourne (2018) report on a population of >100 feral horses in the Steinkopf area of the Northern Cape province, and suggest that there may be significant competition with domestic livestock in that area. Throughout the world, feral horses cause degradation and a decline in ecological integrity (Porfirio et al. 2017). Affects would be context-dependant, but as work in Australia shows there will likely be degradation of the environment. Like donkeys they compete with livestock and native animals for food and space, spread invasive plants and diseases, foul or damage waterholes and cause erosion (Australian Government 2011). Hagen and Kumschick (2018) described horses as having Major environmental impact, but only Moderate socio-economic impact. They are not listed as invasive alien species in the Regulations.

5.3.5 *Dama dama* (Fallow Deer)

Fallow Deer are native to Iran and Iraq and were introduced to South Africa from Europe in the mid-1800s to Cape Town (prior to the oft-cited movement by CJ Rhodes, Skead et al. 2011). This population appears to have been moved around the Cape region, so that by 1970 Fallow Deer covered much of the Western and Northern Cape, and these populations have expanded significantly (Skead et al. 2011), and are now present in all provinces except Limpopo (Picker and Griffiths 2011). Fallow deer are the most widely sold alien ungulate species in South Africa (Spear and Chown 2009a). This species is an opportunistic browser, likely to severely impact native vegetation when densities are high, by ingestion and trampling (Picker and Griffiths 2011). Regulations now prohibit the movement of fallow deer without permits. Consequently, permits for the movement of fallow deer are second highest for mammals (after Red Lechwe, *Kobus leche leche*), but only 11 game farms are permitted to stock them (van Wilgen and Wilson 2018). The Regulations list fallow deer as a Category 2 invasive species. Their relative impacts have not been formally assessed using EICAT or SEICAT (Blackburn et al. 2014; Bacher et al. 2018). One of the best known populations on Robben Island is currently the subject of control (see Chap. 23, Holmes et al. 2020), and are noteworthy for unusual dietary behaviours including ingestion of large amounts (up to 2 L) of plastic (C. Wilke pers. comm.), stranded kelp, newspaper or cardboard and even a rabbit carcass (Sherley 2016).

5.3.6 *Hippotragus equinus* (*Roan Antelope*)

Roan antelope have been imported into South Africa under permits. However, hybridisation occurs between sub-species (Ansell et al. 1971), so after the establishment of *H. e. koba* from West Africa, a moratorium was placed on the movement of roan antelope in South Africa, and a genetic study investigated the spatial genetic structure in roan antelope across their African range. Alpers et al. (2004) provided evidence for the existence of two Evolutionary Significant Units (ESU), based on both mitochondrial and nuclear data. The first corresponds to the West African animals (*H. e. koba*), whilst the East, central and southern African animals formed the second ESU, essentially combining *H. e. equinus*, *H. e. cottoni*, and *H. e. langheldi* into a single genetic group.

It has been estimated that only 300 roan antelope are living in the wild in South Africa, while the remainder (~3500) are ranched on farms (Havemann et al. 2016). Moreover, much of the ranched stocks are now extralimital to the natural distribution of *H. e. equinus*, which only naturally occurs in northern areas of Limpopo province (Kruger et al. 2016). The popularity of this species in the game industry has given rise to concerns for its genetic integrity, as imported *H. e. koba*, from West Africa (Castley et al. 2001), are known to have hybridised with native *H. e. equinus* with resulting hybrids. This has led to the listing of list *H. e. koba* as a Category 2 species in the Regulations, and many conservation authorities now require genetic testing before permits are granted to move Roan antelope between provinces.

5.3.7 *Rusa unicolor* (*Sambar Deer*)

Sambar Deer were introduced to the Groote Schur estate in Cape Town in the 1880s, and from there made their way to Table Mountain (Picker and Griffiths 2011). Their population persists in the wooded areas of Orange Kloof and they have also been seen at the base of the Twelve Apostles. No control programme is in place, and they are not thought to cause serious impact. They are not listed as invasive species in the Regulations.

5.3.8 *Hemitragus jemlahicus* (*Himalayan Tahr*)

Himalayan Tahr are invasive on the Table Mountain section of Table Mountain National Park, where they cause erosion to paths and damage vegetation. A small number of animals were escapees from the Cape Town zoo in the 1930s (Picker and Griffiths 2011), where they quickly scaled the fence. Numbers have varied since their introduction and sporadic investments in control (Davies et al. 2020; Chap. 22).

This species is particularly prominent for the conflicts that it has evoked over control programmes (Zengeya et al. 2017).

5.3.9 *Capra hircus* (Goats)

Goats originate from the Iranian highlands and since domestication have been spread around the world. No introduction date is known for the South African population. Apart from the established population on the Prince Edward Islands (Greve et al. 2020; Chap. 8), feral populations are assumed to exist throughout South Africa. This species has been assessed as having Massive environmental impacts through damage to vegetation while feeding, and minimal socio-economic impacts (Hagen and Kumschick 2018). Although listed as Category 1a under the Regulations, it is not listed as an invasive species on the mainland.

5.3.10 *Oryctolagus cuniculus* (European Rabbit)

Rabbits were deliberately introduced to Robben Island with the intention of forming a breeding population as a ready source of meat. Historical records from 1652 (see Skead et al. 2011), suggest that several consignments of rabbits were introduced to the island without success until 1658, when successful reproduction was first noted. A year later, the rabbits were so abundant that van Riebeeck considered that it would be difficult to exterminate them. Interestingly, historical records suggest that van Riebeeck was aware that the species should not be introduced to the mainland in case it became a pest. Indeed, when he left the Cape he cautioned his successor not to release any rabbits on the mainland. In 2009, the same rabbit population on Robben Island was estimated to exceed 24,000 individuals (de Villiers et al. 2010). Reduction of vegetation on the island, is thought to have driven individuals to start climbing trees to feed on vegetation at heights up to 4 m (Sherley 2016). However, an ongoing effort has removed around 13,000 animals, and no rabbits have been seen on the island for more than 1 year (C. Wilke pers. comm. February 2019; Davies et al. 2020, Chap. 22).

Rabbits have been introduced to all islands off the South African coast, and still occur on Jutten, Dassen, Vondeling, Schaapen, Bird and Seal Islands (Cooper and Brooke 1982). Brooke et al. (1986) suggested that rabbits remain unsuccessful on the mainland as there are too many natural predators.

The populations of rabbits on two islands in the Langebaan lagoon (Schaapen and Meeuw) were the subject of ecological studies in the 1960s, which suggest severe repercussions for the natural vegetation, and the birds that nest on the islands (Gillham 1963). Of note is that the rabbits on Schaapen Island are currently all albino (Cooper and Brooke 1982). Cooper and Brooke (1982) further note that by 1977 the rabbits on Meeuw Island had become extinct. Rabbits have been assessed

as having Massive environmental impacts through damage to vegetation while feeding, and moderate socio-economic impacts (Hagen and Kumschick 2018). They are listed as invasive species under the Regulations when they occur on offshore islands.

5.3.11 *Rodentia*

Globally, invasive rodents threaten agricultural food production and act as reservoirs for disease (Stenseth et al. 2003). One of the most important impacts of rats in South African urban areas are those of zoonotic diseases (see van Helden et al. 2020, Chap. 10), including leptospirosis, plague (caused by the bacillus *Yersinia pestis* transmitted from rats via fleas to humans), and toxoplasmosis in humans (Taylor et al. 2008). They also carry several co-invasive parasites (Julius et al. 2018a, b). *Bartonella* and *Helicobacter* have been found in all three species of *Rattus* in South Africa. For example, a survey of rats in formal and informal housing in Durban found that the rodents carried toxoplasmosis and leptospirosis, but not plague (Taylor et al. 2008). It has also been suggested that, in South African urban areas, zoonotic disease prevalence may increase due to the compromised immune systems of HIV/AIDS patients (van Rensburg et al. 2011).

5.3.11.1 *Mus musculus* (House mice)

House mice were likely introduced to southern Africa through early shipping. There are no early records that specifically relate to this species, and its distribution is now cosmopolitan in South Africa, and sub-saharan Africa (Monadjem et al. 2015). Most studies on this species relate to South Africa's sub-Antarctic islands, where impacts are massive, and these are covered elsewhere (Greve et al. 2020, Chap. 8). On the mainland, its impact appears to be mostly socio-economic (moderate) (Hagen and Kumschick 2018), including spoiling of stored foods. Most occurrence records are associated with building and are apparently scant elsewhere (e.g. Avery 1992). It should not be forgotten that the introduction of mice and rats has been followed in many instances by the introduction of cats to control them, and their impacts may therefore be related. House mice are listed as Category 1b in terms of the Regulations when they occur on offshore islands.

5.3.11.2 *Rattus rattus* (House Rats)

House rats were likely introduced to South Africa in pre-historical times (700–800 AD; Deacon 1986). However, genetic lineages collected in Cape Town suggest that, unlike animals collected on South Africa's south coast that are related

to those of East Africa and Madagascar and are affiliated to Indian haplogroups, rats in Cape Town belong to a haplogroup from current-day Myanmar, Thailand, Cambodia and Vietnam region (Aplin et al. 2011). These two genetic groups suggest multiple introductions to South Africa, via East Africa and direct from the Middle East or India, and chromosomal differences suggest that they remain independent races. House rats were reported to be abundant on Robben Island from 1614 (Crawford and Dyer 2000). The house rat has invaded considerably into South Africa, becoming firmly established in agricultural and urban settings, although it has also been found in forested environments, away from human settlements (Monadjem et al. 2015). However, rats have been found to competitively exclude native mice from homes in rural subsistence settings (Monadjem et al. 2011), such that they are the dominant rodent in and around rural homesteads (Taylor et al. 2012; Themb'alilahlwla et al. 2017).

5.3.11.3 *Rattus norvegicus* (Brown Rat)

Brown Rats were likely introduced to South Africa via ship traffic between Asia and Europe in the seventeenth century, although there are no records to indicate the date of introduction (Skead et al. 2011). It is a strongly commensal species and its distribution is assumed to remain coastal, associated with port and urban areas. However, this species has also been identified in Gauteng province (Bastos et al. 2011; Mostert 2009) presumably originating from coastal areas. This extension of their distribution may have occurred through airfreight (Picker and Griffiths 2011).

5.3.11.4 *Rattus tanezumi* (Asian House Rat)

Asian House Rats, *Rattus tanezumi*, were previously thought to be absent from Africa, but were identified by molecular methods in 2005 (Bastos et al. 2005). This species appears to be widespread throughout both South Africa and Swaziland (Bastos et al. 2011), despite the fact that ecological niche modelling had suggested the climate of South Africa to be unsuitable, based upon its current range (Monadjem et al. 2015). The Asian house rat originates in South-East Asia, and is not considered to have the same high impact as *R. rattus* and *R. norvegicus*, but, considering it is a more recent invasion, its distribution should be monitored for signs of adaptation and growing impact.

5.3.11.5 *Sciurus carolinensis* (Grey squirrel)

Grey Squirrels were deliberately introduced to Cape Town by CJ Rhodes around the turn of the twentieth century (Smithers 1983). Despite more than 100 years since their introduction, this species has not spread beyond the south-western Cape.

Dispersal relies on the presence of alien trees, especially pines (*Pinus*) and oaks (*Quercus*), which were earlier historical introductions (Richardson et al. 2020, Chap. 3). The natural dispersal of these animals was facilitated by deliberate movements by people into Swellendam and Ceres (see Smithers 1983). By 1920, the Cape Provincial Government recognised squirrels as vermin, paying three pence per head (Skead et al. 2011). Squirrels can reach high densities in urban settings with 10–50 per ha in their native areas (Parker and Nilon 2008). Socio-economic impacts of squirrels include damage to pine nut crops, vegetable and fruit crops, and even telephone cables (JM pers. obs.). Most of the impacts of squirrels are thought to be socio-economic, but their sub-lethal and indirect effects on avifauna may be substantial (Bonnington et al. 2013), as they are known nest predators (Hewson et al. 2004). Today, squirrels are revered by many members of the public, and they are only recognised by the Regulations in specific contexts (in association with fruit farming).

5.4 Aves

5.4.1 Invasive Birds in South Africa

There are at least 92 alien bird species that have been introduced to South Africa, with only a minority having become established ($n = 18$) or invasive ($n = 14$) (van Wilgen and Wilson 2018). A suite of birds were introduced to South African towns by European colonists of the eighteenth and nineteenth centuries, seeking to make their surroundings more familiar, as colonists did in many temperate parts of the world (Long 1981; van Rensburg et al. 2011; Duncan et al. 2003).

In South Africa, invasive birds are unusual in all being strongly commensal with humans, without viable populations in natural ecosystems (Richardson et al. 2011b). The spread of native birds into novel (especially urban) areas is not explicitly covered in this chapter (but see Potgieter et al. 2020, Chap. 11), but the success of some species is notable as it is based on the modifications associated with agricultural and urban environments (Symes et al. 2017).

For example, Cattle Egrets, *Bubulcus ibis*, and the Blacksmith Lapwing, *Vanellus armatus*, both arrived in the Cape in the 1930s. Hadedda Ibis, *Bostrychia hagedash*, expanded into the Cape Region in the 1980s (Macdonald et al. 1986), and their population has grown considerably as trees and lawns have proliferated in urbanising areas of a biome which is otherwise largely free of trees and grasses (Duckworth et al. 2010, 2012; Singh and Downs 2016). Urbanisation has been found to have a homogenising effect on the avian fauna of South African cities, with both native and alien birds increasing in density as a result of alien species (van Rensburg et al. 2009).

5.4.2 *Anas platyrhynchos* (*Mallards*)

Mallards have been introduced around the world as domestic and sporting birds (Champagnon et al. 2013; Long 1981). The first individuals sighted in the wild in South Africa were around 1980 in Gauteng and the Western Cape, and are presumed to be escapees from private collections. In South Africa, Mallards are reported to hybridise with the Yellow-billed Duck, *A. undulata* (Dean 2000), and this formed the basis for the listing of this species in the Regulations as Category 2b and therefore the need for control (van Wilgen and Wilson 2018; Davies et al. 2020, Chap. 22), and an impact of Major due to hybridisation with other species in the genus *Anas* (Evans et al. 2016). A genetic study, using microsatellite markers of Mallards, Yellow-billed Ducks and putative hybrids, demonstrated that hybridisation is indeed taking place, but that the direction of hybridisation is into the Mallard population, most commonly with Mallard females and Yellow-billed Duck males (Stephens et al. 2020). This suggests that national control of mallard ducks may be necessary to effectively protect the genetic integrity of Yellow-billed Ducks.

5.4.3 *Passer domesticus indicus* (*House Sparrows*)

House sparrows are believed to have been introduced to South Africa from India by sugar cane workers who brought them as pets. They have expanded their range considerably since the 1950s when they were mainly confined to KwaZulu-Natal, and the population has expanded across South Africa and into all neighbouring countries in southern Africa. House Sparrows are an example of an opportunist, commensal species. In Pietermaritzburg, House Sparrow density was found to be positively related to heavily transformed land use types, such as shopping malls (Magudu and Downs 2015). As they appear not to impact on native birds, and are not predators, this species is listed in the Regulations as Category 3, and is considered to have a moderate impact due to competition with other small passerines (Evans et al. 2016).

5.4.4 *Fringilla coelebs* (*Chaffinch*)

Chaffinches originate in Europe, western Asia and North Africa but were introduced to Cape Town in the 1890s by C J Rhodes as part of his attempt to make the Cape more like his homeland. Currently, this species is most commonly seen on the Cape Peninsula, although birds have been seen as far as Somerset West. Given the 130 years of establishment, it seems unlikely that this species will spread. This species is not listed as invasive under South African legislation, and its impact has not been assessed due to a deficiency of data (Evans et al. 2016).

5.4.5 *Alectoris chukar* (*Chukar Partridge*)

Chukar Partridges were introduced to Robben Island in 1964 after six birds were confiscated by customs officials (Picker and Griffiths 2011). They have a large native range from eastern Europe to northeastern China. Invasive populations occur in New Zealand and a large part of the western USA. The Robben Island population is the only remaining population in South Africa, and is self-sustaining, and may even be growing following the reduction in the feral cat population (see Davies et al. 2020, Chap. 22). Its impact is considered to be moderate due to hybridisation with other partridge species (Evans et al. 2016), although impact on Robben Island is thought to be negligible (van Wilgen and Wilson 2018). This species is listed under the Regulations as Category 2 on the mainland, and 1b on offshore islands.

5.4.6 *Columba livia* (*Rock Doves*)

Rock Doves (aka Common Pigeons) are now widespread in most major urban areas of southern Africa (Little 1994). This species often forms flocks with native Speckled Pigeons, *C. guinea*, but studies suggest that the resources used by Rock Doves do not overlap with Speckled Pigeons (Little 1994). The invasion of Common Pigeons is complicated by their use as pets and in sport (pigeon racing), and escapees from captive collections regularly supplement invasive populations. This has led to a split in public perception where pigeons are seen both as pests (e.g. regarded as flying rats), or an important component of urban wildlife (Cox et al. 2018; Harris et al. 2016). In South African cities, building managers place deterrents to stop individuals roosting and nesting, but most people in the buildings regard these measures as unnecessary (Harris et al. 2016). Common pigeons are considered to have a moderate impact due to the spread of disease to native species (Evans et al. 2016), but are not listed as invasive species under the Regulations in the region. Pigeons are known to carry a considerable burden of parasites (Mushi et al. 2000), including paramyxovirus (Pienaar and Cilliers 1987). Pigeons undoubtedly carry West Nile Virus, although the presence in invasive populations of *C. livia* in South Africa is ambiguous, although they likely act as reservoirs during outbreaks (Jupp 2001).

5.4.7 *Starlings* (*Genus Sturnus*)

Two bird species of the Sturnidae family are top avian invaders both globally and regionally: Common Starlings, *Sturnus vulgaris*, and Common Mynas, *Sturnus* (formerly *Acridotheres*) *tristis*. Their range expansion and evolutionary shifts in morphology of populations have been studied extensively and are the subject of Box 5.1.

Box 5.1 Invasive Common Starlings and Common Mynas

Both Common Starlings *Sturnus vulgaris*, and Common Mynas, *Sturnus tristis* have not fully exploited their potential niches in southern Africa and are still expanding eastwards and northwards. Of the estimated 2.38 billion birds and 3.87 million on average per species for the region, the two invasive starlings (Common Starling: 3.15 million; Common Myna: 1.08 million) are comparable with the average of 2.52 million each of the 14 native Sturnidae species (Hui et al. 2009). Sturnidae species are medium sized, *c.* 100 g, and highly detectable due to their conspicuous features and flocking behaviours. Both species are dietary generalists and commonly occur in urban areas and farms, with no feasible control measures planned. Common starlings are often seen with Pied Starlings (*Spreo bicolor*) and Wattled Starlings (*Creatophora cinerea*) in mixed flocks; in contrast, Common Mynas are bold and particularly aggressive during feeding and roosting (Hockey et al. 2005).

A number of studies have explored the population genetics, dispersal strategies and morphological traits of both species during their range expansion in the region (Berthouly-Salazar et al. 2012a, b, 2013; Hui et al. 2012; Phair et al. 2018). In particular, the invasion dynamics of the two species have supported the two contending mechanisms behind boosted/accelerating invasive range expansion (Hui and Richardson 2017): frequent long distance dispersal (LDD) and spatial sorting. Frequent LDDs are often captured by a leptokurtic fat-tailed dispersal kernel (Kot et al. 1996; Ramanantoanina et al. 2014), whilst spatial sorting of individuals with stronger dispersal abilities at the advancing range edge could leave behind a shift of dispersal-related traits from the introduction point to the range front (Shine et al. 2011). The core-edge comparison of morphological traits for Common Starlings sampled across South Africa shows little signs of spatial sorting of wing morphology, but instead reveals associations of resource competition traits (bill morphology) with distance to the introduction location (Phair et al. 2018). This is similar to the pattern of Common Starlings in North America (Bitton and Graham 2015) but contrasts with detected spatial sorting of wing morphology in Australia (Phair et al. 2018). Genetic analyses of Common Starlings in South Africa have confirmed strong genetic connectivity between core and edge populations, supporting frequent LDDs behind boosted range expansion (Berthouly-Salazar et al. 2013). The acceleration of range expansion of Common Starlings in South Africa is linked to increased contact with changing precipitation regimes (Berthouly-Salazar et al. 2013), supporting the “good stay, bad disperse” rule identified for Common Starlings in Britain (Hui et al. 2012). The detected spatial sorting of bill morphology reflects altered selection forces imposed by different environmental heterogeneity (Phair et al. 2018), also pointing out potential trade-offs between dispersal and foraging traits that could offset the pattern of spatial sorting of dispersal traits (Brown et al. 2013).

(continued)

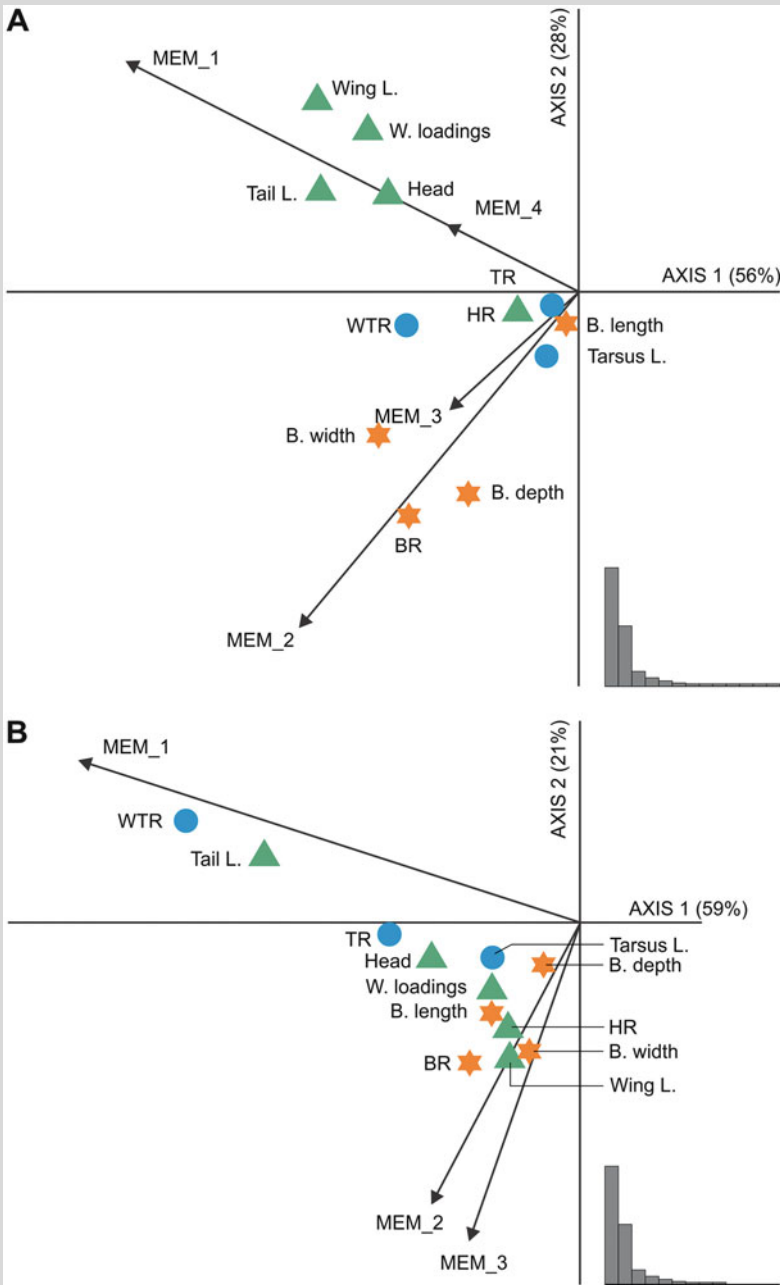
Box 5.1 (continued)

For Common Mynas in South Africa (likely for *A. t. tristis*) a significant correlation was detected between distance to Johannesburg and both dispersal and cognitive traits (Berthouly-Salazar et al. 2012b). Furthermore, sex-biased dispersal in Common Mynas amplifies the spatial sorting of dispersal traits in females (stronger dispersers), specifically the wing morphology (and head size, a qualitative proxy for brain size and thus cognitive abilities), but weakens the pattern in males (figure below). As dispersal strategies are typically linked to mating systems, resulting in resource defence in monogamy where males take the lead role in acquisition and defence of resources and thus receive considerable benefits by remaining philopatric. However, this also makes males more susceptible to predation, and consequently favour aggression-related traits such as morphological variation in tails for male mynas. Sex-biased dispersal also leads to less balanced sex ratios in core populations (e.g. sex ratio is 0.45 for birds within 250 km radius to Johannesburg versus 0.49 for birds beyond the radius). No strong spatial sorting patterns were detected for the subspecies *A. t. tristoides*, with no morphological traits correlated to the distance from Durban (Berthouly-Salazar et al. 2012b). Dispersal-related traits often become homogenised once the range expansion stops so that while the spatial sorting influences morphological variation in expanding populations, its effect will be diluted once populations reach their equilibria. Since the introduction to Durban pre-dates the introduction to Johannesburg by nearly 30 years (Hockey et al. 2005), the Durban expansion has potentially filled up most suitable habitats and reached the distributional equilibrium. In addition, distinct environmental characteristics of these two introduction points could have differentially influenced their expansion. Johannesburg is located within the grassland biome of South Africa, whereas Durban is located within a subtropical thicket that extends along the east coast of the country. While the open grassland or savanna may be more conducive to dispersal, the thicket and coastal forests surrounding Durban but also the Drakensberg mountain ridge seems impenetrable and may have contributed to prevent high levels of dispersal from this coastal introduction point. Factors of habitat quality could affect non-dispersal-related foraging traits. Specifically, urbanisation can modify the quality and type of food resources and therefore influence bill shape (bill length and depth) (figure below). Primary productivity (and thus the habitat quality and food resources) was found to significantly influence the head ratio and bill ratio in both sexes (Berthouly-Salazar et al. 2012b).

Overall, frequent LDDs often work for invasive species that are strong dispersers, while spatial sorting normally acts upon invasive species with poor dispersal ability (Hui and Richardson 2017). The invasion of Common Starlings in South Africa supports the role of frequent LDDs, while the invasion of Common Mynas the role of spatial sorting.

(continued)

Box 5.1 (continued)



Results from the environmental and morphological analysis using the MSPA redundancy analysis for females (a) and for males (b) of Common Mynas. Eigenvalues are shown as

(continued)

Box 5.1 (continued)

insets. Triangles indicate traits related to flight, circles indicate traits related with tarsus, and stars indicate traits related with bill. *W* wing, *B* bill, *WTR* wing-to-tail ratio, *HR* head ratio, *BR* bill ratio, *MEM* axis from Moran's eigenvectors mapping. Note, the spatial predictors *MEM_1* and *MEM_4* are associated with the distance from Johannesburg whilst the spatial predictors (*MEM_2* and *MEM_3*) are related to the distance from Durban and other environmental factors of habitat quality. From Berthouly-Salazar et al. (2012b), reproduced with permission

5.4.7.1 *Sturnus vulgaris* (Common Starling)

Common Starlings are widespread throughout Eurasia, and the South African population stemmed from 18 birds captured in England during winter (potentially overwintering birds from the European continent) and released at Cape Town in 1897 by CJ Rhodes. The species only became widespread in the Western Cape by 1950 and has gradually expanded into the Eastern Cape in the 1960s and KwaZulu-Natal in the 1970s (Hockey et al. 2005) (Box 5.1). This species is listed by the Regulations as Category 3, and it is considered to have moderate impact due to competition (Evans et al. 2016).

5.4.7.2 *Sturnus tristis* (Common Myna)

The Common Myna is native to India, central and south Asia. In South Africa there are two subspecies (Hockey et al. 2005): *S. t. tristis* was introduced to Johannesburg in 1938 from India and Sri Lanka, but only became established in the region in the 1980s, and *S. t. tristoides* that was introduced to Durban from Nepal to Myanmar regions in 1888, escaping from captivity in 1902 (Peacock et al. 2007). Common Mynas are distributed in transformed lands with high human density, where populations can reach hundreds of thousands (Peacock et al. 2007). From their initial release in Durban, populations have spread north-west to Gauteng province, now occupying much of KwaZulu-Natal and Mpumalanga (Box 5.1). New records published suggest that the invasion of this species is ongoing, with populations moving south toward Bloemfontein with short distance movement, such that nearly half of the entire country is colonised (Broms et al. 2016). Importantly, mynas have not reached the winter rainfall area of South Africa, where they may heavily impact on fruit production and the viticulture industry (Gumede and Downs 2019), but the ongoing expansion suggests that their arrival is inevitable. The Common Myna is listed in the Regulations as Category 3, and moderate impact due to competition and predation (Evans et al. 2016).

5.4.8 *Psittacula krameri* (*Rose-Ringed Parakeet*)

The Rose-ringed Parakeet is a popular caged bird that has established populations in 35 countries on five continents (Menchetti et al. 2016; Shwartz et al. 2009). Native to a broad swath of central and West Africa, and the Indian subcontinent, individuals have been seen in South Africa ever since caged birds were brought here. Records include 1850 for Cape Town and birds were common in Durban by the 1970s (Picker and Griffiths 2011). In South Africa, Rose-ringed Parakeet populations are rapidly expanding their range (Symes 2014), with animals established in Gauteng (Roche and Bedford-Shaw 2008), Pietermaritzburg, Cape Town, Steytlerville (in the Eastern Cape), and Durban where the population currently occupies $\sim 730 \text{ km}^2$ with four main roosts of between 20 and 100 birds (Hart and Downs 2014).

Physiological experiments on caged South African parakeets suggest that these birds are tolerant of a wide range of ambient, especially low temperatures, and are therefore equipped to cope with a variety of climatic situations in the country (Thabethe et al. 2013). However, occurrence of the Rose-ringed Parakeet in South Africa is currently best predicted by human density (Hugo and van Rensburg 2009). Despite their known impacts as an invasive species, these birds are still popular as cage birds in South Africa, and 55 of 78 properties issued with notices under the Regulations were for Rose-ringed Parakeets, with the majority of these being for traders (van Wilgen and Wilson 2018). Similarly, the Rose-ringed Parakeet was the second-highest species that had permits issued for use of a listed invasive species within South Africa for (108) (van Wilgen and Wilson 2018). Impacts include competition with other cavity-nesting birds and frugivores, as well as potential impacts on certain agricultural crops (Menchetti et al. 2016). In addition, Rose-ringed Parakeets are known reservoirs of chlamydiosis and other diseases (Menchetti and Mori 2014). Their impact is considered to be Moderate based on competition and predation mechanisms (Evans et al. 2016). Details of their control are covered by Davies et al. (2020), Chap. 22. See also Potgieter et al. (2020), Chap. 11 for their impact in the urban context.

5.4.9 *Corvus splendens* (*House Crows*)

House Crows are native to the Indian sub-continent, but have invaded countries in the Middle East, East Africa (Kenya, Tanzania, Mozambique) and offshore islands (Madagascar, Mauritius, Reunion and Seychelles Nyári et al. 2006). The first published records of House Crows arriving in South Africa date to the 1970s: Durban in 1972, and Cape Town in 1979 (Dean 2000; Hockey et al. 2005). These birds are known to use marine vessels to move from colonies on the east coast of the continent into South African ports. In the urban context, House Crows are aggressive toward people, and thrive in densely populated areas where litter and food waste collects. In Cape Town, they were reported to harass primary and pre-school

children, and butchers in informal settlements (L. Stafford pers. comm.). They damage crops, domestic poultry and have the potential to transmit disease (e.g. various prion diseases such as scrapie and chronic wasting disease). Their impact is considered to be Moderate based on competition and predation mechanisms (Evans et al. 2016), and they are listed as invasive species under the Regulations as Category 1b. Details of their control are covered by Davies et al. (2020), Chap. 22. See also Potgieter et al. (2020), Chap. 11 for their impact in the urban context.

5.4.10 *Pavo cristatus* (Common Peafowl)

Common Peafowl (aka Peacocks) originate from the Indian continent and Sri Lanka, but have become frequently stocked in residential estates around the world. In South Africa, these birds have now been recorded in every province and individuals are frequently seen outside of areas where they were originally stocked. Although many populations may be maintained and be considered domestic or partially feral, of particular note is a population on Robben Island which was introduced in 1968, and has since maintained itself without further interference. To date there have been no studies on this species in South Africa, but it has been identified as a conflict species. Some residents love these showy birds, while others loathe them, their faeces and their loud calls (Zengeya et al. 2017). Individuals are fed by residents, but birds are not confined and have spread into neighbouring areas. There are vineyards where flocks of peafowl cause considerable damage to the vines and fruit. The City of Cape Town has received many requests to remove them from peri-urban areas where they occur, although they currently are not listed in the Regulations. Evans et al. (2016) considered impact of this species to be of Minimal Concern with respect to competition and interaction with other invasive species.

5.5 Reptilia

5.5.1 *Invasive Reptiles in South Africa*

Currently, all invasive reptiles in South Africa are considered accidental releases because of inadvertent movement of eggs or adults. However, there are increasing numbers of reptiles imported (or bred locally) as pets, seen in urban and even rural settings. South Africa has sightings of escaped Red-eared Slider, *Trachemys scripta*, which have been made in Durban, Johannesburg and Pretoria, but breeding has not been recorded (Branch 2014a). The most commonly encountered alien reptiles are Corn Snakes, *Pantherophis guttatus*, with 10 of a total of 45 sightings of alien reptiles in South Africa (Bates et al. 2014). This is perhaps in part because they have conspicuous colouration and are unlike most other snakes in the region. Other

commonly-spotted escaped pets are Bearded Dragons, *Pogona vitticeps*, Boa Constrictors, *Boa constrictor*, Californian King Snakes, *Lampropeltis californiae*, and Sinaloan King Snakes, *L. triangulum*. Of particular concern is the escape of various alien pythons which have been confused with native Rock Pythons, *Python sebae*, and which can hybridise with the native species. Moreover, some popular pet snakes appear to be reproductively flexible with parthenogenetic capabilities (Booth and Schuett 2016; Booth et al. 2012). A rise in popularity of pet reptiles in South Africa has been previously flagged as a potential emergent invasion issue (van Wilgen et al. 2010). Other than the species discussed below, a number of other translocated and introduced populations of reptiles are noted by Brooke et al. (1986), but there is no known change in their current status and so have not been reported on here.

5.5.2 *Hemidactylus mabouia* (*Tropical House Gecko*)

Tropical House Geckos are endemic to Central and East Africa, extending south into the northeast of South Africa. It is one of five invasive *Hemidactylus* species that now have global distributions; the others being *H. brookii*, *H. frenatus*, *H. garnotii* and *H. turcicus*. Mediterranean climates (such as that in South Africa's winter rainfall zone: see Wilson et al. 2020, Chap. 13) are suitable for most of these species, and it has been predicted that *H. brookii* will likely expand its range into areas currently occupied by *H. mabouia* (Weterings and Vetter 2018).

Populations of *H. mabouia* species have invaded West Africa, the Caribbean, South America and Florida (Weterings and Vetter 2018). Invasions have resulted in displacement of native geckos in Florida and Curaçao (Dornburg et al. 2016; Short and Petren 2012, but see also Williams et al. 2016). The first extralimital records in South Africa for this species are for East London and Port Elizabeth in the 1980s (Brooke et al. 1986; Rebelo et al. 2019), although, like the common dwarf gecko (see below), first sightings in Port Elizabeth may be biased to the activities of a keen resident herpetologist and the true dates for other cities may be earlier than reported. Both are presumed to have arrived with seaborne cargo (Brooke et al. 1986). Many populations are known outside of the native range in South Africa, including a range expansion along the coastal areas towards East London (Bourquin 1987), and jump dispersal to almost all urban areas in the central and south of the country. Introductions to Simon's Town and Gordon's Bay in the Western Cape in 1962 and 1976 respectively, were deliberately made from Sierra Leone (Brooke et al. 1986). While it is not known whether displacement of native geckos is occurring, there are anecdotal observations of displacement of the Marbled Leaf-toed Gecko, *Afrogecko porphyreus*, in Cape Town (which itself has an established population in Port Elizabeth: Rebelo et al. 2019). The impact of the Tropical House Gecko has not been formally assessed, and it is not listed in the Regulations.

5.5.3 *Lygodactylus capensis* (*Common Dwarf Gecko*)

This species is a day gecko, which like the Tropical House Gecko is native to the north-eastern areas of South Africa but its commensal habits have led to it invading many urban areas of the country (Bauer et al. 2014), such that it has been described as South Africa's most successful invasive reptile (Rebello et al. 2019). The earliest records date to around 1956 in Port Elizabeth, although other introductions may have been earlier (Rebello et al. 2019). Expansions in peri-urban areas of Port Elizabeth and Bloemfontein have been rapid, while that in Cape Town has been comparatively slow. The introduction of this species to Cape Town is thought to have originated with the establishment of a population in a nursery. Hitch-hiking and stowaways as adults and eggs are likely to be the pathway of invasions (Rebello et al. 2019). For example, a crate from Kruger National Park is presumed to be the source of a population which established in Addo Elephant National Park in the 1970s (Branch 1981). Branch (2014b) noted that they are rarely found away from man-made structures, although the number of sightings in natural settings is rising (Rebello et al. 2019). As no other day geckos are native to the invaded areas, there is unlikely to be any intra-guild competition. The common dwarf gecko is not known to be invasive elsewhere in the world, although it is a likely candidate, and its impact has not been assessed. Common Dwarf Geckos are not listed in the Regulations.

5.5.4 *Indotyphlops braminus* (*Flowerpot Snake*)

The Flowerpot Snake originates from southeast Asia, but has become invasive all over the world and is, after the Red-eared Slider, the world's most widely-distributed reptile (Kraus 2008). Ironically, this was one of the first snakes recorded from South Africa (in 1838), and only recognised as an invasive in 1978 (Measey and Branch 2014). Since that time, new populations have been found at the coast in Durban (Brooke et al. 1986), and inland in the Western Cape. It is noteworthy that this species reproduces parthenogenetically, and so easily establishes new populations on introduction. The impact of these small thread snakes has not been assessed anywhere, and the species is not listed in the Regulations.

5.6 Amphibia

5.6.1 *Hyperolius marmoratus* (*Painted Reed Frog*)

Painted Reed Frogs were detected in Villiersdorp, Western Cape in 1997 and in Cape Town in 2004 (Davies et al. 2013). A subsequent genetic study showed that these animals consisted of individuals that were extending their range from the Eastern

Cape, and translocated animals from Mpumalanga, with the first records around 1995 (Tolley et al. 2008). Davies et al. (2013) explained how Painted Reed Frogs have been able to overcome their historical range limits by using a combination of human-mediated jump dispersal and artificial impoundments. This has allowed these frogs to expand their niche into novel environmental space, not occupied in the native range (Davies et al. 2013). The permanence of the dams mitigated the influence of historical climatic barriers that previously prevented movement into drier and more thermally variable habitats (Davies et al. 2019). Importantly, their model suggests that the invasion is ongoing, with only around a quarter of potential sites occupied, a result that was corroborated in a niche-modelling exercise on the same species, which signified range disequilibrium (Davies et al. 2019). Painted reed frogs in their novel range were found to exhibit plasticity of temperature limits and metabolism, which may provide benefit in drier and more thermally variable habitats of its novel range (Davies et al. 2015). The painted reed frog poses considerable risk should its populations be moved to other suitable climates globally. In the urban environment, age-structured and landscape resistance models suggest that this species would be able to rapidly colonise garden ponds, quickly saturating an area of 50 km² within 10 years of its introduction to a new site (Vimercati et al. 2017a).

5.6.2 *Sclerophrys gutturalis* (*Guttural Toad*)

The Guttural Toad was deliberately introduced to Mauritius and from there to Reunion in the 1920s as a biological control for mosquitoes (Telford et al. 2019). The same species was first recorded in Constantia, a suburb of Cape Town, in 2000 (de Villiers 2006), with the presumption that individuals were transferred unintentionally with a consignment of aquatic plants from Durban (de Villiers 2006; Measey et al. 2017). Genetic investigation into the origin of all three invasions suggests that all of these explanations are correct. Moreover, invasions into Mauritius and (then) Reunion, also appear to be derived from the Durban area, but have much greater genetic diversity than the Constantia invasion as a result of the deliberate introduction (Telford et al. 2019). The rapid movement from Durban, in South Africa's summer rainfall zone, to Constantia in the winter rainfall zone (see Wilson et al. 2020, Chap. 14), and the short period this species has had to adapt, are of considerable interest. Field data show that Constantia animals are significantly more dehydrated than Durban populations (Vimercati et al. 2018). However, the toads were able to withstand dehydration by hunkering down into a water-conserving posture. The invading toads also performed better in endurance trials, by moving much farther than animals from their native Durban when dehydrated. Lastly, invading toads were able to withstand cooler conditions than Durban animals (Vimercati et al. 2018). This rapid adaptation to a novel climate means that Guttural Toads could invade more areas with a similar climate.

The Constantia population has been subjected to control measures (see Davies et al. 2020, Chap. 22) and is also mentioned in the context of urban invasions (Potgieter et al. 2020, Chap. 11). Modelling of the Guttural Toad invasion has provided insight into population dynamics, which translate into practical implications for control. For example, the density-dependent nature of tadpoles and metamorphs (Vimercati et al. 2017a, b) means that contracted workers can concentrate on removing adults and juveniles, saving considerable expense and time spent in private properties.

5.7 Future Perspectives for Invasive Vertebrates

Our cumulative records for terrestrial vertebrates look unlike those reported by Picker and Griffiths (2017) (Fig. 5.2a), most likely as they were missing some introduction dates and ‘domestic exotics’ such as the geckos and frogs. Their inclusion here suggests that contrary to the conclusion of Picker and Griffiths (2017), terrestrial vertebrate invasions in South Africa have seen the biggest rise during the last 150 years. We found that the proportion of deliberate to accidental introductions was skewed toward deliberate introductions, although the trend is moving from deliberate to accidental (Fig. 5.2b). Similarly, species in the last 150 years have Asia as the most common donor region. However, most recently, is the arrival of ‘domestic exotics’ (Guo and Ricklefs 2010), species that have part of their native and introduced range within South Africa. Studies to date (Telford et al. 2019; Tolley et al. 2008) suggest that all invasions originate from populations within the country.

Many of the species reviewed here still have the capacity to increase their distribution and invasive impact in South Africa, and so reports of low or no impacts mentioned above are probably not static. Although it is encouraging that only a single successful twenty-first century invasion is recorded here (Asian House Rat, *R. tanezumi*), this situation may reflect a level of invasion debt in vertebrate species (Rouget et al. 2016), commensurate with the increased levels of trade (Faulkner et al. 2017). Many of the impact levels (EICAT and SEICAT, see Blackburn et al. 2014; Bacher et al. 2018) noted above have not been assessed in the South African context, but this is required for high-ranking species such as feral pigs, donkeys, feral cats, horses, fallow deer, goats and house crows. This sets an important research agenda for the region.

Interactions between invasive vertebrates (and other invasive species) are not well documented in South Africa, but have been implicated with the term ‘invasion meltdown’ when facilitation occurs. Conversely, some invasive species can repel others or simply have negative impacts, such as Rose-ringed Parakeets attacking and killing House Rats (Hernández-Brító et al. 2014).

There are also signs that the numbers of invasive vertebrate species are rising (Fig. 5.2a). Of concern is the growing demand for ornamental and caged birds in

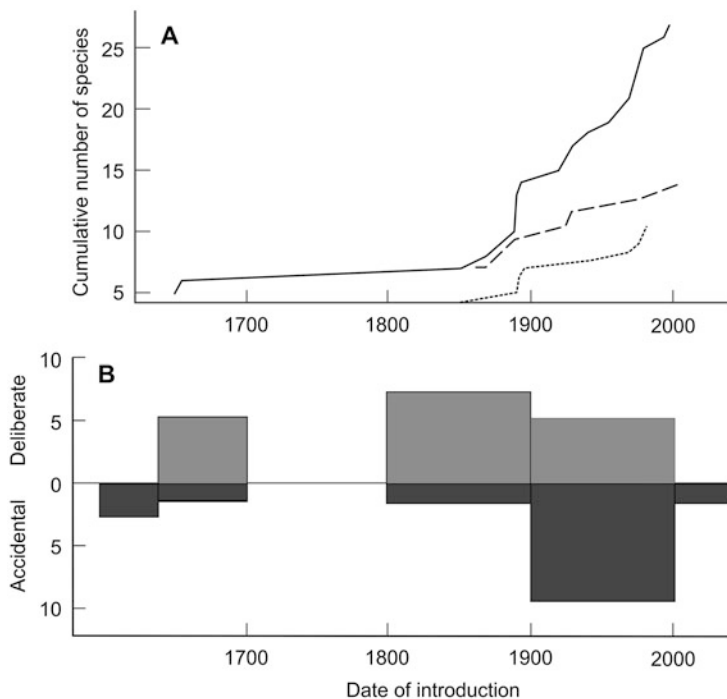


Fig. 5.2 (a) The cumulative number of invasive vertebrate species (solid line) shows previously undescribed trend of quick growth rates from the mid-1900s. Sharp increases in the late 1800s are attributable mostly to birds (dotted line), while mammals continue to show a steady growth (dashed line). (b) There is a trend away from deliberate introductions and towards a growing number of accidental introductions

South Africa, and other parts of the developing world (Goss and Cumming 2013), which may see a rise in invasive species. Similarly, the rising demand for reptiles as pets, and the rising numbers of (especially) snakes (with the threat of hybridisation to native pythons) found, suggests that we will soon see newly-established populations of alien species from the pet trade.

Lastly, we emphasise here the need for consideration of domestic exotics with formal lists of invasive species. NEM:BA is exemplary in its flexibility to formally list species that are native in some parts of the geopolitical area of South Africa, but invasive in other parts, as invasive. This has provided important legislative power to help to control invasions (see Chap. 23).

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