

Chapter 27

South Africa as a Donor of Alien Animals



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Abstract This review provides the first assessment of animal species that are native to South Africa and invasive elsewhere in the world. While around a twelfth of all naturalised plants in the world are native to South Africa, there are very few examples of South African native marine, terrestrial, or freshwater animals becoming invasive elsewhere. We provide a narrative of each of the 34 cases that we could find. Three of these species, the Common Waxbill, *Estrilda astrild*, the Mozambique Tilapia, *Oreochromis mossambicus* and the African Clawed Frog, *Xenopus laevis*, were widely traded, and introduced on several continents with invasive populations becoming the subject of substantial research. Most other species are poorly documented in the literature such that it is often not known whether South African populations are the source of invasions. These species demonstrate the same trend in pathways of animals entering South Africa, moving from deliberate to accidental through time. The role of mavericks, individuals whose deliberate actions wilfully facilitate invasions, is highlighted. While South Africa has acted as an important bridgehead for the invasions of forestry pests, crayfish, fish and amphibians on the continent, it is clearly not a major donor of animal invasions, but rather a recipient. This could be due to South African ecosystems being fundamentally more invulnerable, or South African fauna showing reduced invasiveness, though it is likely that substantial differences in historical pathways also played a crucial role.

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27.1 Introduction

Some animals from South Africa are well known invasives around the world. They have been the subject of numerous studies, and are among the best known invaders of their taxa. For example, the African Clawed Frog, *Xenopus laevis*, is the third most studied invading amphibian (van Wilgen et al. 2018), and the Mozambique Tilapia, *Oreochromis mossambicus*, has been heralded as one of the most widely introduced fish species globally (Pullin et al. 1997; Froese and Pauly 2019, Fig. 27.1). However, there seem to be few examples and, to our knowledge, there has been no attempt to compile a comprehensive list of fauna donated from South Africa, which are established elsewhere in the world. Thus, our aim in this chapter is to compile such a list, and determine the mode and tempo of these introductions. In addition, we attempt to document the pertinent literature providing a brief overview of the native and invasive distribution, the pathway, and impacts of each species.

One of the ways in which South Africa is a donor of alien animals is by the bridgehead effect. This is where alien species introduced to South Africa have become established, and South Africa has subsequently become a source of invasion



Fig. 27.1 Some of the highest impacting invasive species that South Africa has spread around the world. (a) The African clawed frog, *Xenopus laevis* being electro-fished in a river in Portugal, (b) the Mozambique Tilapia, *Oreochromis mossambicus*, within its native range, (c) the Common Waxbill, *Estrilda astrild*, and (d) the South African Mantis, *Miomantis caffra*

for these species into other countries (Lombaert et al. 2010; Faulkner et al. 2017b). Therefore, in addition to native species, we also consider some of the alien species that have been moved through South Africa.

27.2 Methods

To identify species, we started with a list provided in Picker and Griffiths (2011), and augmented this with published databases of known alien species (Welcomme 1988; Long 2003; Lever 2005; Kraus 2009; Dyer et al. 2017; (Froese and Pauly 2019); WRiMS 2019), our expert knowledge and consultation with key researchers (see acknowledgements).

In many cases, the provenance of invasions are not known, and since most invasive species have widespread distributions (e.g. Blackburn and Duncan 2001; Tingley et al. 2010), we included every species that has an established population and that has part of its native range within South Africa. This inclusive approach has been followed elsewhere (see Pyšek et al. 2020, Chap. 26). However, species that have multi-continental distributions (including a portion of South Africa), and which may in addition have some introduced populations, were not included (but these birds are included in Supplementary Table S27.1). Where it was known that the population did not come from South Africa, we note this in the textual account for the species and in Supplementary Table S27.1.

We only considered species where populations were known to have become established (*sensu* Richardson et al. 2011) outside their native range. We did not include any re-introductions of species within or contiguous with their native range (e.g. zebras, rhinos, giraffe, elephants, etc. see Long 2003), or those that might be extralimital but within South Africa (see Maciejewski and Kerley 2014). We excluded species that had been introduced but are no longer known to be present (although some are mentioned when pertinent, below). We also excluded any species from South Africa that had deliberately been introduced elsewhere as biocontrol agents. In this way, we attempt to provide a species list of fauna from South Africa that are currently established elsewhere in the world.

27.3 Results and Discussion

Our study suggests that, unlike plants (Pyšek et al. 2020, Chap. 26), South Africa is clearly a net receiver of alien animals. A total of 629 alien animal species are recorded as established in South Africa (van Wilgen et al. 2020, Chap. 1, Table 1.1), but only 34 native South African species are established in other countries (see Table 27.1). Moreover, many of the animals (at least 20%) detailed in this chapter likely did not have their origins from South Africa (Table 27.1).

Table 27.1 South Africa is a net recipient of invasive animals across taxonomic groups

Group Taxon	Number of invasive species donated	Number of invasive species received	Bridgehead for invasions	References
Terrestrial vertebrates	26	30	1	Measey et al. (2020, Chap. 5)
Invertebrates	3	466	4	Janion-Scheepers and Griffiths (2020, Chap. 7)
Freshwater animals	1	77	24	Weyl et al. (2020, Chap. 6)
Coastal species	4	56	0	Robinson et al. (2020, Chap. 9)

Data on the numbers of animal species native to South Africa and invasive elsewhere in the world are from this chapter. Species were included only when evidence was well documented and the species is believed to still be established (i.e. the numbers below will likely be under-estimates). Note that even if species have South Africa as part of their native range, invasive populations elsewhere in the world need not have originated from South Africa (i.e. South Africa was not a “donor”)

There are several possible reasons for the observed difference between plants and animals donated from South Africa. Firstly, databases on alien animals are confined largely to vertebrates, and established populations of invertebrates are likely to be far greater than we record here, but difficult to detect in the literature. One justification for this assertion is that the most numerous taxa represented in our list are the birds, which are probably the best taxon reported on in databases and the literature (e.g. Duncan et al. 2003). However, despite providing a large number of candidate species, very few are known to have been introduced from South Africa (4 out of 14 in Supplementary Table S27.1). This may mean that our chapter gives an unrealistically low representation of South African non-avian animals alien in other countries. Secondly, the scientific literature tends to be biased toward European and North American hubs, and poorly reflects alien species in Africa (e.g. van Wilgen et al. 2018). Thirdly, it could be that South African animals have few areas in the world for which they are suitable, or that they are particularly not invasive. This seems unlikely as South Africa has many areas of the world that are climate matched (Richardson and Thuiller 2007; van Wilgen et al. 2020, Chap. 1), and there are a considerable number of domestic exotic animals (see below). Lastly, South Africa underwent a hiatus in global trade from the United Nations resolution (no. 1761) in 1962 due to restrictions imposed by many countries reacting to the then apartheid regime. Sanctions only began to be lifted in the early 1990s (Evenett 2002). This period relates to the start of an exponential increase in global trade (Federico and Tena-Junguito 2017), and commensurate invasions (Seebens et al. 2017). It is possible that as trade from South Africa during this time was reduced, the contribution of animal species did not reach its potential levels. It would be important therefore to ensure through legislation that the introduction debt (*sensu* Rouget et al. 2016) built up during this time does not result in a future glut of animal invasions from South Africa.

27.3.1 Pathways

Only three species (*Estrilda astrild*, *Oreochromis mossambicus* and *Xenopus laevis*) are related to deliberate commercial trade that has resulted in many invasive populations globally. Their footprints are large, and have been the focus of considerable research. The other species are all introduced to one or two areas in single events, and have attracted considerably less research attention.

Stowaways are particularly unusual in our list, but include geckos, spiders, butterflies and mussels. Only two examples of contamination occur in our list, both of marine organisms. Other species were deliberately transported, with the animals subsequently escaping or being intentionally released in new areas.

Whether it was Frank Hibben, the man responsible for introducing Gemsbok to New Mexico, or Pablo Escobar, whose Hippos now inhabit Columbian rivers, many of the pathways recorded here reflect maverick individuals who wanted these African animals in their own countries. Some, such as the Mauritian port director, Gabriel Regnard, introduced many alien species in an attempt to ‘improve’ the diversity of the local fauna. Others were motivated by conservation and poverty alleviation, such as the movement of freshwater fish in the 1930s from hatcheries in Jonkershoek and Pirie to English speaking countries in southern and eastern Africa. Douglas Hey, then Director of Nature Conservation of the Cape Province, presided over the importation and breeding of large numbers of fish species sent to him from Europe and North America (*cf* van Wilgen 2020, Chap. 2). His belief that he was aiding communities throughout the region did not require any evidence in the form of economic justification. Instead, his position as Director allowed him to continue experimenting with new species for decades. Hey was also responsible for supplying tertiary and research institutes with African Clawed Frogs (van Sittert and Measey 2016). The actions of individuals continue to impact invasions in the region, as seen by the relatively recent activities of Adrien Piers introducing Red Claw Crayfish into Swaziland (and their subsequent invasion into South Africa and Mozambique: Nunes et al. 2017b; Weyl et al. 2020, Chap. 6), Zambia and from there to Zimbabwe (see Welz 2017). While legislation may prevent many potential introductions, the role of mavericks driven by their own convictions will remain a problematic issue for the introduction of animals from South Africa and elsewhere. This is especially true now that e-commerce has opened up the possibility for many more species to reach individuals with more conviction than time to consider potential outcomes of their actions (*cf* Faulkner et al. 2020, Chap. 12).

27.3.2 Non-South African Origins

For many of the species listed below, we are not sure that the population that became invasive originated in South Africa. In some cases (e.g. Hippopotamus, Gemsbok and African Sacred Ibis), we know that it did not: 20% of cases on our list (Supplementary Table S27.1). But we have still included an account here because

these species are known to have distributions that include South Africa (*cf* Pyšek et al. 2020, Chap. 26). Compared with many other countries on the continent, South Africa has considerable trade relations with the rest of the continent, and the world through several international airports and three large shipping ports (Faulkner et al. 2017a). This affords it ample opportunity to have become an important donor. However, the major pathways implicated in the spread of South African vascular plants around the world (horticultural trade, agricultural trade; Pyšek et al. 2020, Chap. 26), are absent for South African animals. Much of the trade in large mammals appears to have gone through the auspices of zoos and private collections (e.g. Hippopotamus, Gemsbok).

27.3.3 *South Africa as a Bridgehead for Invasions*

South Africa is recognised as having had a long history as a major commercial hub for southern Africa, and in some cases for the continent (Faulkner et al. 2017a). There are documented historical examples of how South Africa has acted as a bridgehead for invasions elsewhere on the continent (Lombaert et al. 2010). Below, we provide some examples of this movement. Although not exhaustive, they serve to show the importance of this effect, which is arguably greater than that South Africa has had for direct donations of alien animals.

27.3.3.1 *Forestry Pests*

The spread of insect pests of trees is an increasing problem in Africa (Graziosi et al. 2019). Bridgehead effects are the case for insect pests of forest plantations in South Africa, especially those infesting species of *Eucalyptus* (Faulkner et al. 2017b). South Africa is one of only a small number of countries where insect pests of *Eucalyptus* have been reported for the first time outside their native range and subsequently spread to other countries (Hurley et al. 2016). One example is the Eucalypt Snout Beetle, *Gonipterus* sp. 2 (formerly *Gonipterus scutellatus*), which was first reported in South Africa in 1916 (Tooke 1955), and over the next decades reported in other African countries as well as southern Europe (Mapondera et al. 2012). In fact, the majority of alien insect pests of eucalypts in sub-Saharan Africa were first reported in South Africa (Hurley et al. 2017). These include the Bronze Bug, *Thaumastocoris peregrinus*, the Eucalypt Longhorn Beetles, *Phoracantha* spp., and the Bluegum Psyllid, *Ctenarytaina eucalypti*. However, assumptions on the inter- or intra-continental spread of alien species based on first report data is not always accurate, as sampling effort can differ considerably between countries (Hurley et al. 2017).

The introduction pathways of forest insect pests from South Africa into other countries is generally not known. However, likely pathways for the introduction of wood boring insects such as Eucalypt Longhorn Beetles, included as stowaways on

wood packaging material, and the timber trade (Meurisse et al. 2018). Likely pathways for leaf feeding insects such as the Bronze Bug and the Bluegum Psyllid, include contaminants on plants, and as stowaways on various commodities (Meurisse et al. 2018). These insects can also be transported as stowaways on people and their luggage, for example the Bronze Bug has been reported to attach itself to peoples' clothing and hair. For neighbouring countries, introduction may occur simply by natural dispersal, assisted by the wide distribution of the host trees (eucalypts) in these countries.

A number of insects native to South Africa have expanded their host range to include non-native plantation trees, namely eucalypts and pines. Examples include the Chrysomelid beetles, *Colasposoma* spp., the Lymantrid Moth, *Euproctis terminalis*, and the Saturniid Moth, *Imbrasia cytherea* (Roux et al. 2012). The probability of these insects spreading to other countries seems likely to increase due to their increased population and the availability of these hosts.

27.3.3.2 Crayfish

Four species of freshwater crayfish have been introduced into South Africa for aquaculture: the Smooth Marron, *Cherax cainii* in 1976, the Common Yabby, *C. destructor* and the Redclaw Crayfish, *C. quadricarinatus*, in 1988, and in the ornamental trade *Procambarus clarkii*, the Red Swamp Crayfish in 1982 (Nunes et al. 2017a). Some of these crayfish species were then further moved introduced from South Africa into neighbouring countries. For example, *C. destructor* and *C. quadricarinatus* were imported from South Africa in 1992 to Livingstone in Zambia (van den Audenaerde 1994; Mikkola 1996). The introduction of *Cherax destructor* failed but *C. quadricarinatus* managed to establish in the wild (Mikkola 1996). *Cherax quadricarinatus* was deliberately moved from Livingstone to several areas in Zambia, but was only recently confirmed as established in the Kafue River system (Douthwaite et al. 2018). Other bridgehead invasions by *C. quadricarinatus* into several river systems in middle Zambezi and Limpopo River catchments have occurred as a result of both intentional and accidental introductions from Swaziland. For example, *C. quadricarinatus* was also introduced into the Kafue River in 2001 from Swaziland, and it has since appeared in the upper and middle Zambezi sub-catchments after escaping from nearby fish farms (Douthwaite et al. 2018). Elsewhere, *C. quadricarinatus* escaped from aquaculture facilities in Swaziland and as a result of downstream spread and subsequent dispersal, it is now established in several river systems in Swaziland, South Africa and Mozambique (Nunes et al. 2017b). The *C. quadricarinatus* invasions in southern Africa, including ongoing invasion in South Africa, are some of the worst on the continent. Its presence in upper catchments of major rivers such as the Zambezi River is likely to ensure a sustained influx of propagules into downstream river systems and adjacent river systems such as Okavango Delta are now exposed to a major invasion risk (Nunes et al. 2016).

27.3.3.3 Frogs

Xenopus laevis was moved extensively around the world (Box 27.1), but the global trade was an order of magnitude smaller than the regional trade in frogs for academic research in southern and eastern Africa (van Sittert and Measey 2016). While the majority of these animals were intended for dissections, it seems likely that many would have been released. Most of these institutions would have been within the native range of this species (see Furman et al. 2015), and thus any introductions would likely manifest as genetic introgression with native populations. Measey et al. (2017) report the finding of one such example, with the genetic signature of *X. laevis* from Jonkershoek (near Stellenbosch, Western Cape) mixed with animals from a local clade on the university campus in Port Elizabeth.

Box 27.1 A Model Species Turned Invader—*Xenopus laevis*

The African Clawed Frog, *Xenopus laevis*, has a particularly interesting history that have carried this rather atypical anuran into laboratories of tertiary institutions the world over, eventually rising to the status as the ‘model amphibian’ (Tomlinson et al. 2005), and directly resulting in the deliberate or accidental release of animals on four continents (Measey et al. 2012). In 2018, there were nearly 1000 publications focused on this species from diverse subject areas including Biochemistry, Genetics and Molecular Biology; Agricultural and Biological Sciences; Medicine; Neuroscience and Pharmacology, Toxicology and Pharmaceuticals. The African Clawed Frog has achieved this remarkable success as individuals are easily maintained in laboratories, and importantly will reproduce throughout the year when stimulated with hormones. This allows easy access to embryos and tadpoles that are pivotal to the understanding of many research fields. This frog was the first vertebrate to be cloned, leading to the Nobel Prize of Sir John Gurdon in 2012. Gurdon et al. (1958) showed that nuclear information present in cells from the intestines of tadpoles are pluripotent, growing into new individuals when implanted into an enucleated egg.

Described by the French naturalist Daudin in 1802 from a specimen of unknown provenance and no longer in existence, the African Clawed Frog became a well known animal of curiosity over the next few decades. Live specimens arrived from South Africa in European capitals and were prominently displayed in large water filled jars. By the end of the century, animals were breeding in captivity, and the development of their midwater suspension feeding larvae was being studied (Gurdon and Hopwood 2003).

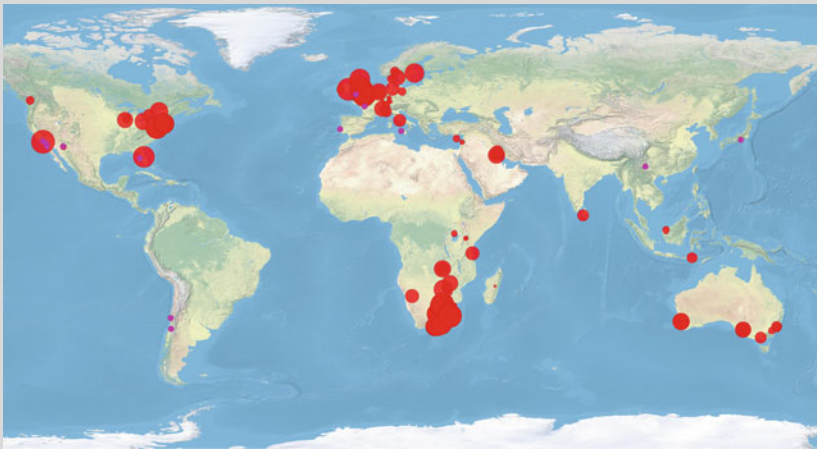
In South Africa, tertiary institutions were being formed at the beginning of the twentieth century, and *X. laevis* was the amphibian of choice for dissection, due to their high density in local dams and ease of maintenance prior to use. Bringing large numbers of this frog into the laboratory led to its local use in physiology research. So it was that when British biologist, Lancelot Hogben

(continued)

Box 27.1 (continued)

arrived in Cape Town in 1927, *X. laevis* was already in the Physiology Department (Gurdon and Hopwood 2003). Hogben recognised the potential of using *X. laevis* for studies of endocrinology. In 1930 he published a paper in which he explained how ovulation could be induced in *X. laevis* females through injection of ox pituitary (Hogben 1930). This soon led to the realisation that urine from a pregnant woman could induce the same effect due to the presence of gonadotrophins, and very quickly the Hogben test became a standard for pregnancy testing in the United Kingdom and then throughout the British empire.

The use of *X. laevis* for pregnancy testing necessitated the export of thousands of live animals from the Cape. In the 1940s, the Cape Provincial Administration's Department of Nature Conservation, under Douglas Hey (see van Wilgen 2020, Chap. 2), saw the need for these frogs to be supplied, and included them among their cultures of alien fish that they were breeding and disseminating. That decade they shipped 32,000 *X. laevis* overseas, but a larger quantity were being distributed around British colonies in southern and East Africa for dissections in universities (van Sittert and Measey 2016). The 1950s saw the peak in demand and supply of *X. laevis* from Jonkershoek (near Stellenbosch in Western Cape Province) supplying overseas and domestic orders, and Pirie Fish Hatchery (near King Williams Town in Eastern Cape Province) supplying tertiary institutes in southern Africa (van Sittert and Measey 2016), totalling some 150,000 animals (figure below).



The destinations of African Clawed Frogs, *Xenopus laevis*, shipped around the world from South Africa between 1940 and 1970 (data from van Sittert and Measey 2016) shown proportionately in red circles. Purple dots show the locations of currently known invasive populations of *X. laevis*

(continued)

Box 27.1 (continued)

The movement of large quantities of animals from South Africa quickly saw populations establish in other parts of the world. The first was found on Ascension Island in the 1940s, although the provenance of this population is unknown and it is now thought to be extinct (Loveridge 1959; Measey et al. 2012). By the 1960s, populations had established in several locations in the southern US states, Chile and in the UK. In the 1980s more populations began being recorded in Europe (Measey et al. 2012), and there are still more being discovered (e.g. Peralta-García et al. 2014; Hill et al. 2017). Although the historical pathway detailed above is recognised as donating much of the genetic stock (Lillo et al. 2013; Lobos et al. 2014; but see de Busschere et al. 2016), it has been suggested that laboratory populations have been responsible for secondary movements of many captive (and subsequently released) laboratory stocks (van Sittert and Measey 2016; Sousa et al. 2018). More recently, the pet trade has been implicated in the movement in excess of 100,000 albino animals annually into the US (Measey 2017). The first established albino population of *X. laevis* has now been discovered on the Chinese mainland (Wang et al. 2019). This marks a shift from invasive populations principally associated with the scientific trade to those moved for the pet trade.

27.3.3.4 Fish

Several species of trout (e.g., Brown Trout, *Salmo trutta*, and Rainbow Trout, *Oncorhynchus mykiss*), Black basses (e.g., Largemouth Bass, *Micropterus salmoides*), and Cyprinids (e.g., Common Carp, *Cyprinus carpio*) were introduced into South Africa and from there to several countries in southern Africa (de Moor and Bruton 1988; see Welcomme 1988 for a complete list of 24 species). For example, *S. trutta* was introduced into South Africa in 1892 from England from where it was then introduced to Swaziland (1915), Lesotho (1907–1914), Zimbabwe (1907), Tanzania (1934) and even the sub-Antarctic Marion Island (1964) (Weyl et al. 2017; Box 12.1 in Faulkner et al. 2020). Similarly, *C. carpio* was distributed to Botswana, Lesotho (1965), Namibia, Zambia (1980), and Zimbabwe (1925) (Ellender and Weyl 2014), and *Micropterus salmoides* into Namibia and Zimbabwe (1932), Botswana and Lesotho (1937) and Swaziland (1947) (Bell-Cross and Minshull 1988).

27.3.4 *Domestic Exotics*

It seems likely that South Africa will continue to be a donor of alien animal species to the rest of the world, but the trends reported here suggest that these species will be mostly transported accidentally, rather than the large scale deliberate introductions of (mostly vertebrates) seen in the past. One indication of which South African species may pose a future threat of invasion elsewhere in the world are those that are currently domestic exotics (*cf* Guo and Ricklefs 2010). Examples include the Painted Reed Frog, *Hyperolius marmoratus*, the Guttural Toad, *Sclerophrys gutturalis* and the Common Dwarf Gecko, *Lygodactylus capensis* (see Measey et al. 2020, Chap. 5). We show that many South African species alien elsewhere are currently domestic exotics in South Africa, with invasive or extralimital populations moving between biomes (see Measey et al. 2020, Chap. 5). Domestic exotic species appear to be a logical starting point for raising concerns and preventing movements of South African animals elsewhere in the world, and can provide useful information for risk and impact assessments.

27.3.5 *Taxonomic Considerations*

Of the taxa that we included below, some groups were conspicuous by their absence, and we discuss here some of these taxonomic considerations.

There are many South African animals, and in particular the mammals, which have been introduced into public and private zoological collections around the world. Many are kept outdoors but despite incidental escapes, suggesting some level of appropriate climatic tolerance, few have been able to become established outside of their native range. It is of particular note that South Africa has a high diversity of ungulates (Spear and Chown 2009), and that the Gemsbok and three suriformes (Hippopotamus, Bushpig and Warthog) have been reported as established elsewhere in the world. Many other populations of South African ungulates exist in zoos and private collections, which have international stud books and means of breeding between them such that they do not need to be re-supplemented from native stocks. These captive populations are for the most part carefully managed. South Africa is also a centre of diversity for the Afrotheria, an African clade of mammals with diverse morphological characteristics. None are known to have established populations outside of their native ranges.

The taxonomy of Green Monkeys, listed by Long (2003) as *Cercopithecus aethiops*, and established in the Caribbean and Cape Verde, has now been updated such that the introduced West African Green Monkey, *Chlorocebus sabaeus*, is the introduced species while the South African Vervet Monkey, *Chlorocebus pygerythrus*, has not been introduced.

Birds have been studied intensively and their current distributions as well as introductions are well recorded so that the databases are particularly advanced

(Duncan et al. 2003; Carrete and Tella 2008; Dyer et al. 2017). It is maybe for this reason that our list has more birds than any other taxa (41%). Several wide-ranging bird species (over two or more continents) that have part of their distribution in South Africa, also have invasive populations (Dyer et al. 2017). These have not been included in the list of species in this chapter (but see Supplementary Table S27.1). Of the other birds, many of the introductions are from species with distributions across most of sub-Saharan Africa, and South Africa is not thought to be the source of the established population. Only a small number of South African birds have been traded and have formed established populations around the world. Of these, only the Village Weaver, *Ploceus cucullatus*, Cape and Yellow Canaries, *Serinus canicollis*, *S. flavigentris*, and the Common Ostrich, *Struthio camelus*, are known to have been introduced from South Africa (although the Ostrich may have been supplemented with stock from Sudan). Others are now extinct, like the Blue-breasted Cordon-bleu *Uraeginthus angolensis* on St. Helena (Lever 2005).

Some birds, such as the Pied Crow, *Corvus albus*, undergo short movements out of their range and pairs have occasionally been observed staying for long periods North of the Sahara, and as far as Spain and Portugal (Pepe 2017). Some breeding populations of this species have already been extirpated (Dyer et al. 2017). There is one example of a breeding pair in Morocco, and another of an individual on a rubbish dump in Jodhpur, India (Saikia and Gaswami 2017). It has been suggested that the pathway for some of these far reaching individuals may be ship assisted, as is the case for the House Crow, *Corvus splendens* (see Measey et al. 2020, Chap. 5), and if this is the case then it seems likely that Pied Crows pose a considerable future threat for becoming invasive in many parts of the world. A number of South African reptiles are in the pet trade and are known to survive after release. For example, Krysko et al. (2011) documented a number of species found released (but not established) in Florida, including the Leopard tortoise, *Stigmochelys pardalis* (see Measey et al. 2020, Chap. 5), Turner's Thick-toed Gecko, *Chondrodactylus turneri* and Bibron's Thick-toed Gecko, *C. bibronii* (there are suggestions that an established population of *C. bibronii* does occur in Florida, but this could not be verified).

South Africa has three species of amphibians that have established populations outside of the country. It is noteworthy that one (the Guttural Toad) is also invasive in South Africa as a domestic exotic (Measey et al. 2020, Chap. 5), and two (the Guttural Toad and the African Clawed Frog) are the subject of control measures in the country (Davies et al. 2020, Chap. 22). In addition, there are some incidental records of South African amphibians, such as Fornasini's Spiny Reed Frog, *Afraxalus fornasini* in Florida (Krysko et al. 2011).

While South Africa has a high diversity of marine and freshwater fishes (Skelton 2001), very few have been introduced elsewhere in the world. Of those that have, detailed below, it has not been confirmed that South Africa was the source of the alien populations. However, South Africa has played an important role as a bridge-head for invasions elsewhere on the continent (see Sect. 27.3; Weyl et al. 2020, Chap. 6).

The East African Lowland Honey Bee, *Apis mellifera scutellata*, is native to a large part of East and southern Africa, including much of South Africa. This sub-species is often preferred over the European sub-species, *A. m. linguistica*, as it produces a larger quantity of honey. However, *A. m. scutellata* have a reputation for being more aggressive. Many apirists have hybridised the two sub-species to produce so-called ‘Africanized honey bees’, and these bees are extensively used and invasive in Brazil and North America. As this is a hybrid of a sub-species, we have not included this taxon in our list of alien animals from South Africa.

It should also be noted that there may well be parasites that have travelled with the hosts mentioned in this chapter and have successfully formed their own invasive populations (le Roux et al. 2020, Chap. 14). Although these are not often reported, and invasive populations benefit from enemy release (e.g. Torchin and Mitchell 2004), there are some studies from South African examples. The African Clawed Frog, *Xenopus laevis*, has one of the most diverse parasite faunas, with 20 metazoan parasites within its native range (see references in Schoeman et al. 2019). Some have been found in invasive populations, including the monogenean *Protopolystoma xenopodis* in populations from California, France and Portugal, and the cestode *Cephalochlamys namaquensis* in California and France (Schoeman et al. 2019), however none are known to have moved hosts to local species. Host transfer has been recorded between four out of six monogeneans from introduced *O. mossambicus* to local Chilid fish, *Cichlasoma calliolepis* and *C. fenestratum*, in Lake Catemaco, Veracruz, Mexico (Jiménez-García et al. 2001). We have not included separate accounts for parasites, or included them in our totals.

27.4 Species Accounts

27.4.1 Mammals

27.4.1.1 The Hippopotamus, *Hippopotamus amphibius*

Pablo Escobar, the notorious drug baron, maintained a private zoo in his jungle hideout, Hacienda Nápoles, in Magdalena, between Medellin and Bogota in Columbia. In the 1980s, he introduced three pairs of Hippopotamus from zoos in the US, which began breeding in Hacienda Nápoles and subsequently escaped into the Magdalena River growing to an estimated population of 20 to 40 individuals (Buriticá 2014; Valderrama Vásquez 2012). Hippopotamuses are native to all of sub-Saharan Africa, but are now considered Vulnerable by the IUCN due to habitat change and hunting. Impact of the increasing population in Columbia included attacks on fishermen, killing of livestock, destruction of crops and general fear among the local population, including stopping fishermen from accessing their fishing grounds (Valderrama Vásquez 2012). The control operation is controversial as the hippos are still an attraction at the theme park that was made from Escobar’s home. This has meant that although they pose a very real threat to people living

along the river, culling is rare, and instead one male was castrated and flown back to Hacienda Nápoles by helicopter (Valderrama Vásquez 2012; Restrepo Betancur et al. 2016). Currently, the population at Hacienda Nápoles still exists and females breed with young males that left the group and invaded stretches of the Magdalena River.

27.4.1.2 Common Warthog, *Phacochoerus africanus*

Common Warthogs are native to a large part of sub-Saharan Africa, excluding the Congo basin and the arid western areas of southern Africa. They were first reported from within the Chaparral Wildlife Management Area, South Texas, USA, in 2014 (Tompkins 2015). They are known to have been kept on private ranches in the area, and are thought to have burrowed under these fences to enter into the protected area. Today, Common Warthog are regularly seen on camera traps in the Chaparral Wildlife Management Area together with their offspring (W. Gann pers. comm. May 2019). Currently, there have been no studies made on this population, but their impacts are thought to be similar to the rapidly expanding population of Feral Pigs (*Sus scrofa*; see Measey et al. 2020, Chap. 5) also in the same area.

27.4.1.3 Bushpigs, *Potamochoerus porcus*

Bushpigs are native to a large swathe of eastern Africa, from Ethiopia in the north, to Mossel Bay on South Africa's south coast. They are thought to have been introduced to Mayotte in the Comoros Islands and to Madagascar, but whether they were introduced or dispersed naturally (via rafting on papyrus) is still contested (Long 2003; Oliver 1993). On the one hand, the Malagasy and Comoro forms are so distinct from those on the mainland that they have been named as different subspecies. However, this is not unexpected given the morphological changes that we know invasive populations undergo relatively quickly (see Box 27.2). Others argue that bushpigs were introduced (Vercammen et al. 1993), probably with the movement of peoples to these islands. Such an introduction would have to date to pre-Austronesian times, some 2000 years BP (Blench 2008). Bushpigs are now widespread throughout Madagascar, missing only from the deforested central plateau and major townships (Vercammen et al. 1993). These animals play an important part in the local bushmeat trade (Golden 2009; Randrianandrianina et al. 2010), may contribute significantly to the dispersal of fruits (although probably destroying many, Ganzhorn et al. 1999), and form an important prey item of the threatened Fosa, *Cryptoprocta ferox*. They are also an important reservoir for African Swine Fever (Roger et al. 2001).

Box 27.2 Spatial Sorting of African Clawed Frogs in France

Invasive populations undergoing expansion can evolve life-history traits increasing their capacity to reproduce, disperse, and survive (Wilson et al. 2009; Burton et al. 2010; Stevens et al. 2010). Dispersing individuals at the range edge of an expanding population have been found to differentially allocate resources compared to those at the core (Burton et al. 2010; Bonte et al. 2012; Chuang and Peterson 2016; Travis et al. 2010). The resource allocation influence of life-history traits that are dispersal relevant may result in spatial differentiation of expanding populations, also known as spatial sorting (Shine et al. 2011). Evidence of spatial sorting can be found in a plethora of taxa, including Orthoptera (Simmons and Thomas 2004), Lepidoptera (Hughes et al. 2007; Karlsson and Johansson 2008), Hymenoptera (Léotard et al. 2009), Amphibia (Llewelyn et al. 2010; Brown et al. 2013; Hudson et al. 2015), Aves (see Measey et al. 2020, Chap. 5) and Pinales (Cwynar and MacDonald 1987). If dispersal-relevant traits are inherited, gene expression will accumulate at the range edge. These traits can be morphological, (e.g. larger wing size, Simmons and Thomas 2004; longer legs, Llewelyn et al. 2010), behavioural (e.g. altering movement patterns, Alford et al. 2009), and physiological (e.g. greater endurance, Llewelyn et al. 2010). This results in individuals at the range edge evolving a novel phenotype that is adept for dispersal and differs from that at the core; evolution in space rather than through time (Shine et al. 2011).

In western France, the African Clawed Frog, *Xenopus laevis*, (figure below) was released into the natural environment when a breeding facility for the CNRS closed in the 1980s (Fouquet and Measey 2006). Individuals have been expanding from this single introduction point colonizing water bodies now covering an area $\sim 2000 \text{ km}^2$ (Louppe et al. 2017). An estimated overland spread in the invasive range $\sim 1 \text{ km}$ per year, although dispersal through waterways appears to be much faster (Fouquet and Measey 2006).



An adult African Clawed Frog, *Xenopus laevis*

(continued)

Box 27.2 (continued)

At the edge of the distribution individuals have been found to allocate less resources to reproduction than individuals at the core. Individuals at the edge exhibit a decrease in the relative mass of reproductive organs during the peak of the breeding season (Courant et al. 2017a). Evidence suggests that increased energy resources are allocated to dispersal for edge *X. laevis* individuals (Louppe et al. 2017). Males at the core show better endurance capacity than females due to their relatively longer limbs and lower body mass. At the edge, both males and females have smaller body sizes than those at the core. Frogs from the edge may also have improved swimming performance due to the relative increase in limb length. This would assist in dispersal, increasing dispersal by overland migration and through rivers and streams (Louppe et al. 2017).

The trade-offs displayed by *X. laevis* between reproduction, mobility, and morphology can be constrained by the metabolism of the individual. At the range edge, where individuals display a decrease in reproductive ability and an increase in dispersal (through an increase in mobility), individuals exhibit a lower standard metabolic rate (SMR) (Louppe et al. 2018). At the core of the distribution males display a higher SMR than females, whereas at the edge females displayed a higher SMR than males explaining the differences in endurance capacity between males and females (cf Hulbert and Else 1981). A lower SMR for males at the edge can enhance their ability to allocate resources to dispersal, whereas a higher SMR for males in the core can enhance resources for reproduction. The SMR in females at the edge is lower than females at the core but higher than males at the edge. This indicates that fewer resources are allocated to reproduction at the edge overall for males and females (Louppe et al. 2018).

The allocation of resources to dispersal ability (morphology, endurance, distance travelled) rather than reproduction is expected to influence the growth rate and lifespan of *X. laevis* (e.g. Phillips et al. 2010; Amundsen et al. 2012). However, no differences of growth rate and life span have been found for individuals at the core and the edge (Courant et al. 2019a). This indicates that an accelerated growth rate in individuals is not a dispersal-relevant trait for this expanding population. A higher survival probability has been found for individuals at the edge compared to the core (Courant et al. 2019b). Thus, survival rather than faster development and longer lifespan is displayed by individuals of *X. laevis* at the edge. The spatial sorting of *X. laevis* in western France is evidence of rapid evolution just ~40 years after their introduction (Courant et al. 2019b).

27.4.1.4 Gemsbok, *Oryx gazella*

The Gemsbok, *Oryx gazella*, is native to Namibia, Botswana and northwestern arid areas of South Africa. Between 1969 to 1977, 93 Gemsbok were introduced to White Sands Missile Range, part of the Chihuahuan Desert of New Mexico, USA, from captive-bred stock of unknown provenance. The aim was to increase sport hunting for wealthy visitors (Bender et al. 2003). By the early 2000s, the population had grown to between 3000 and 6000 individuals, and had spread over an area of 15,000 km² in southern New Mexico, to become the most numerous ungulate in the state (Bender et al. 2003). Gemsbok tested were found to have significant infectious diseases, which may affect recovery of native ungulates, including Desert Bighorn Sheep, *Ovis canadensis mexicana*. They have been found to have considerable dietary overlap with another native ungulate, the American Pronghorn, *Antilocapra americana* (Cain et al. 2017).

27.4.2 Birds

27.4.2.1 Common Ostrich, *Struthio camelus*

The Common Ostrich, *Struthio camelus*, has been farmed in South Africa's Karoo since the 1860s, and the similarity between this region and South Australia was generally appreciated and Ostrich farming encouraged and facilitated by the local government (Iwanicki 1985). Birds were mostly imported from South Africa, but there is one notable importation of 12 birds from Sudan that were bred with the South African flock at Yanco Experimental Farm (Hastings and Farrell 1991). The Ostrich industry suffered a collapse in 1914, and the biggest farm near Port Augusta, South Australia, closed in 1916, selling most of its stock. However, some feral birds remained, and these were cared for by the new owners who farmed sheep. The flock north of Port Augusta now occur across at least three very large (30,000+ ha) properties, where they have been present for over 100 years. The total population still probably numbers fewer than 250 birds (perhaps even as low as 100) but they have been in rangeland country since the late 1800s and are most certainly self sustaining (R. Clarke pers. comm.). Despite ostriches being farmed in many other parts of the world, no other established populations are known (Lever 2005). Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.2 Egyptian Goose, *Alopochen aegyptiaca*

The Egyptian Goose (a shelgoose and member of the subfamily Tadorninae) is native to nearly all of sub-Saharan Africa, including all of South Africa. It is invasive in the UK, northeast France, Belgium, the Netherlands, Germany, Denmark and Sweden. Populations are also recorded from the USA, Israel and United Arab Emirates. Egyptian Geese are known to have been introduced to East Anglia in the seventeenth

century as an ornamental waterbird (Lever 2005; Sutherland and Allport 1991; see Kampe-Persson 2010 for a recent review). This became an established population (Sutherland and Allport 1991). From the 1950s onwards, Egyptian Geese were kept in many sites in Europe, but it seems that a population from The Hague began to expand rapidly and colonised all areas of The Netherlands by the end of the twentieth century, showing a classic invasion exponential expansion from the mid-1990s (Gyimesi and Lensink 2012). The Dutch population has spread into neighbouring countries and is currently expanding. Other noteworthy established populations have been documented in the USA states of Texas (Callaghan and Brooks 2016) and Arkansas (Smith and Fames 2012). This species is considered a pest requiring control in many urban areas of South Africa (cf Potgieter et al. 2020, Chap. 11), and may be implicated in movement of propagules of alien species, especially freshwater plants (Reynolds et al. 2015; cf. Hill et al. 2020, Chap. 4). Evans et al. (2016) listed their EICAT impact as Minor due to competition and nutrient loading.

27.4.2.3 Pin-tailed Whydah, *Vidua macroura*

The Pin-tailed Whydah, *Vidua macroura*, is native to much of sub-Saharan Africa but has been introduced to Puerto Rico in the 1960s via the pet trade (Lever 2005). Populations have been seen since the 1990s in California (Garrett and Garrett 2016), and in Florida since the mid-2010s (Greenlaw et al. 2014). This species is an obligate avian brood parasite, and most commonly parasitises the Common Waxbill in its native range (see below). The Pin-tailed Whydah became established in Puerto Rico following accidental releases from the pet trade, and switching to parasitise Orange-cheeked Waxbills, also established on the island (Raffaele 1989). Other established populations are in southern California (and most likely in neighbouring Mexico) and Florida in the USA.

There is concern that this species may occupy a larger area of North America, especially given the existing populations of the Common Waxbill, and the Pin-tailed Whydah's ability to switch hosts (Crystal-Ornelas et al. 2017). Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.4 Laughing Dove, *Spilopelia senegalensis*

The Laughing Dove, *Spilopelia senegalensis*, was introduced to Perth Zoological Gardens in 1898, and subsequently was released and has become widespread in Western Australia following a rapid population expansion in the 1930s (Forshaw 2015). It is not clear from where they originated, but they resemble the sub-Saharan form. This species appears to be a strong human commensal, and it has not spread far from Perth (Forshaw 2015). Laughing Doves are carriers of and form a reservoir for psittacine beak and feather disease, a common viral disease of captive birds in Australia (Raidal and Riddoch 1997). Other populations are recorded from Príncipe Island and Mafia Island (populations on the Mascarene Islands are believed to be

from Asia) (Lever 2005). Evans et al. (2016) listed their EICAT impact as Minor due to disease.

27.4.2.5 Village Weaver, *Ploceus cucullatus*

The Village Weaver, *Ploceus cucullatus*, is native to a large part of sub-Saharan Africa, and in South Africa this species has undergone recent expansion due to its commensal habits (South African Bird Atlas Project). The South African form *P. c. spilonorotus* was introduced to Réunion in 1880 and Mauritius in 1886 (Lahti 2003). It has been suggested that Village Weavers were deliberately released by their owner, Gabriel Regnard (Cheke and Hume 2010). On Mauritius, it is said to have displaced the introduced Cape Canary, *Serinus canicollis*, while both species continue to co-exist on Réunion (Jones 1996). The introduction of this species to Hispaniola is thought to be of the West African form, *P. c. cucullatus* (Wetmore and Swales 1931), and there have been other incidental records and sightings including the southern USA and southern Europe (see Lahti 2003). It is considered to be an agricultural pest, as it nests in large colonies which forage causing crop damage to grain crops. Accordingly, Evans et al. (2016) listed their EICAT impact as Minor.

27.4.2.6 Lesser Masked Weaver, *Ploceus intermedius*

Lesser Masked Weaver, *Ploceus intermedius*, is native to sub-Saharan Africa. It is listed as established in Taiwan, Yemen and United Arab Emirates (Lever 2005). Lesser Masked Weavers are known to breed in Chiba Prefecture, Japan since the 1960s (Eguchi and Amano 2004), with an estimated population around 10,000 breeding pairs (Brazil 2009). There is a somewhat smaller population on Taiwan, China (Brazil 2009). Their EICAT impact is listed as Data Deficient (Evans et al. 2016).

27.4.2.7 Yellow Canary, *Serinus flaviventris*

The Yellow Canary is native to South Africa, Botswana and Namibia. They were introduced to Ascension Island and St. Helena in 1776 (Brooke et al. 1995), where they are still established and said to have caused damage to soft fruit grown there (Lever 2005). Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.8 Cape Canary, *Serinus canicollis*

The Cape Canary, *Serinus canicollis*, is native to southern Africa, and was introduced to a number of islands: St. Helena, Mauritius, Réunion and Tahiti (Brooke et al. 1995). Of these, introduction was only successful on Réunion between 1830 and 1860 (Jones 1996; Cheke and Hume 2010). The 1760 introduction to Mauritius later declined and eventually became extinct (Simberloff and Gibbons 2004). Barré

(1983) states that *S. canicollis* was introduced from South Africa. Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.9 Common Waxbills, *Estrilda astrild*

Waxbills have a long history in the bird trade, with records dating back to the nineteenth century in Brazil and Europe (Cardoso and Reino 2018), and 1820 to St. Helena (Brooke et al. 1995). A more recent introduction to Portugal in 1964 appears to be the source of an invasion on the Iberian Peninsula (Reino and Silva 1998). Common Waxbills in Europe are thought to have been wild-caught in northern Senegal (Sanz-Aguilar et al. 2014). They have a large distribution in sub-Saharan Africa encompassing arid and tropical zones, and including much of South Africa (Stiels et al. 2011). Given their introduction into Portugal and Brazil, it seems likely that some of the original populations were from Mozambique and/or Angola (Cardoso and Reino 2018). Today they are invasive in many regions in Brazil, the Iberian Peninsula (Spain and Portugal) as well as a host of islands within the tropics (Stiels et al. 2011). Due to their widespread introductions across the world, they have been dubbed as the most successful invasive tropical bird (Lever 2005). The Common Waxbill has the potential to be a much greater problem globally, especially in the tropics, but also in the subtropics and some temperate areas, including much of western Europe and southern and western USA and Mexico (Stiels et al. 2011). Their EICAT impact is listed as Data Deficient (Evans et al. 2016), but it has been argued that they have no impact in Europe (Cardoso and Reino 2018). There has been a great deal of research into this species as an invasion model in dispersal, behavioural (e.g. changes in personality) and evolutionary ecology (e.g. changes in ornamentation). Cardoso and Reino (2018) recently compiled an overview of the research on this species.

27.4.2.10 Bronze Munia, *Lonchura cucullata*

The Bronze Munia, *Lonchura cucullata*, is native to most of sub-Saharan Africa, and the eastern portion of South Africa. It was introduced to Puerto Rico in the mid-1500s with slave trafficking (from West Africa), such that it was abundant by the late 1870s (Frahner et al. 2015), but their numbers in some areas are reported to be declining (de Jersey Gemmill 2015). One impact of the Bronze Munia is to act as a reservoir for brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*). The fear is that this, and other introduced birds, could provide a foothold for the Shiny Cowbird to then parasitise native birds (Wiley 1985). Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.11 Yellow-Crowned Bishop, *Euplectes afer*

The Yellow-crowned Bishop, *Euplectes afer*, is native to most of sub-Saharan Africa, but has formed established populations in Europe (Italy, Spain and Portugal:

Carrete and Tella 2008), Florida (USA), Puerto Rico (since the early 1970s), Venezuela and Jamaica (since the late 1980s; Lever 2005). The European populations are thought to have resulted from the trade in wild-caught cage birds (Carrete and Tella 2008). Individuals in Europe are thought to have been wild-caught in northern Senegal in the mid-1980s (Sanz-Aguilar et al. 2014). Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.12 Helmeted Guineafowl, *Numida meleagris*

Helmeted Guineafowl are known to have been introduced to Greece by the fifth century BC, and Italy by the first century AD, with possible introduction into Germany around this same time (Poole 2010). There are records in France dating back to the fifteenth century with animals reaching Britain in the sixteenth century. All of these introductions are associated with using animals as food, for their ornamental feathers and as display animals. During the early stages of introductions, birds remained scarce and highly sought after. Today, this species is raised commercially for the table in many parts of the world. Most of the European populations are extinct, although current records exist for the Canary Islands and Great Britain (DAISIE 2019). Other introduced populations include Japan, Yemen, West Indies, Brazil, Australia, New Zealand, and many islands: Annabon, Ascension, Canary, Cape Verde, Chagos, Comoros and the Mascarenes (Lever 2005; McKinney and Kark 2017). In addition to being invasive elsewhere in the world, they are an extralimital species in the Fynbos Biome of South Africa, where they were introduced in the late 1800s to improve sport-shooting (Brooke and Siegfried 1991; see Measey et al. 2020, Chap. 5).

Controversially, Helmeted Guineafowl have been used as a bio-control agent against ticks carrying Crimean–Congo hemorrhagic fever in Turkey (Şekercioğlu 2013). However, evidence suggests that they are themselves potential hosts for the same ticks they were released to control. Moreover, Helmeted Guineafowl are a known host of Newcastle disease (an important poultry virus), but their EICAT impact is listed as Data Deficient (Evans et al. 2016).

27.4.2.13 African Sacred Ibis, *Threskiornis aethiopicus*

African Sacred Ibis were introduced to Europe from Egypt (from where it later disappeared) in the 1700s, and small populations were maintained until the 1970s when they became popular exhibits in zoological gardens (Clergeau et al. 2010). A zoo in Brittany was the origin of the northern French invasive population, which had reached ~3000 individuals by 2004 (Marion 2013). Similarly, another zoo on the Mediterranean coast was the source of a population there, which was said to have potential predatory impacts on threatened native birds. This prompted a nationwide call for their extermination, and caused conflict with people who argued for their aesthetic quality. Marion (2013) argued that as their principle diet is of invertebrates, they are not the predatory threat that others had claimed (see also Strubbe et al. 2011), although they are opportunistic predators of birds, reptiles, fish and amphibians.

Escapes from zoos also occurred in Spain, the Canary Islands, and Italy, but in these locations numbers have not exceeded efforts to control and contain them (Yesou and Clergeau 2005). Small populations of African Sacred Ibis also occur in United Arab Emirates, Taiwan (Dayuan Township, Taoyuan City County) and the Florida Everglades (Yesou and Clergeau 2005). Evans et al. (2016) listed their EICAT impact is listed as Minor due to predation.

27.4.3 *Amphibians*

27.4.3.1 *The African Clawed Frog, *Xenopus laevis**

African clawed frogs have been widely introduced to laboratories the world over since the 1930s, first for pregnancy testing, then as a model amphibian and most recently as a popular pet species (Box 27.1). Although these frogs are principally aquatic, they readily move between ponds up to distances of several kilometers (Measey 2016; de Villiers and Measey 2017), making their invasions like those of other amphibians and crayfish. Currently, they are known from multiple countries on four continents (Measey et al. 2012). Invasions are relatively well studied in Italy (Sicily: Lillo et al. 2008; Giacalone et al. 2008), Chile (Lobos and Measey 2002; Lobos and Jaksic 2005; Lobos et al. 2013), Portugal (Rebelo et al. 2010; Moreira et al. 2017), UK (Measey and Tinsley 1998; Measey 1998, 2001) and USA (McCoid and Fritts 1980a, b, 1989). Adults are principally predators of aquatic macroinvertebrates (Measey 1998; Amaral and Rebelo 2012; Courant et al. 2017c, 2018a), but there is evidence that they adversely affect native amphibian populations in their introduced areas (Lillo et al. 2011; Courant et al. 2018). Indeed, adults are capable of ingesting a range of vertebrate prey items (Lafferty and Page 1997; Measey et al. 2015). African clawed frogs are assessed as having Major impacts (Kumschick et al. 2017; Measey et al. 2016) using the EICAT scheme. Adults also carry parasites, but invasive populations generally have a reduced parasite diversity (Schoeman et al. 2019). Little work has been carried out on tadpoles, although they were found to respond to novel and historical predators in a similar fashion (Kruger et al. 2019).

The French invasion is noteworthy as it has a higher genetic diversity than any known native site, originating from two genetic clades native to southern Africa (de Busschere et al. 2016). The mixing of these genetic lineages is suggested to be the reason for this population extending beyond the native niche, shifting its realised niche (Rödder et al. 2017). This suggests that in France the mixed lineages have adapted to local conditions and are no longer constrained by its historical niche. This population has already reached the Loire Valley (Louppe et al. 2017), a virtual gateway connecting waterways throughout mainland Europe and more than one million km² of suitable climate space (Measey et al. 2012). Moreover, this estimate is set to increase given climate change scenarios, especially into north-western Europe (Ihlow et al. 2016). Despite the French invasion only being ~40 years old,

this invasion shows many attributes of a population undergoing evolution through spatial sorting (see Box 27.2).

It has been suggested that this species shows an invasion debt of ~15 years (van Sittert and Measey 2016), and with high propagule pressure continuing in the form of shipments for pets (Measey 2017). This species has many traits which appear universally favoured (Measey et al. 2020, Chap. 5). It seems likely that we will continue to see many more invasive populations the world over.

27.4.3.2 The Guttural Toad, *Sclerophrys gutturalis*

The Guttural Toad has a wide distribution in southern Africa, from Ethiopia across Uganda to northern Angola, and across much of Botswana, Zimbabwe, Mozambique and the north and east parts of South Africa (Telford et al. 2019). The first introduction of the Guttural Toad outside their native range was a naive attempt at bio-control for Cane Beetles, *Phyllophaga smithi*, in Mauritius in 1922. They were introduced by the director of the dock management company in Port Louis, Gabriel Regnard (Cheke and Hume 2010). It is noteworthy that after the failure of the Guttural Toad to control the Cane Beetle, Gabriel Regnard tried and failed to introduce the Cane Toad, *Rhinella marina* (from Puerto Rico), on several occasions (Cheke and Hume 2010). Although it is not recorded from where these Guttural Toads were sourced, a genetic study suggests that the most likely source is Durban, South Africa (Telford et al. 2019). Guttural Toads were moved from Mauritius to Reunion around 1927, again as a bio-control agent, but this time against malaria carrying mosquitoes (Cheke and Hume 2010). Following both introductions, these toads quickly colonised the lower areas of each island. They are thought to have a moderate (MO) impact by predation of native snails in Mauritius (Kumschick et al. 2017; Measey et al. 2016), although this is with low confidence as no study has quantified their diet. Guttural Toads are also invasive within South Africa (see Measey et al. 2020, Chap. 5).

27.4.3.3 Clicking Stream Frog, *Strongylopus grayii*

The Clicking Stream Frog is native to a wide area of South Africa across rainfall zones (cf. Fig. 13.2, Wilson et al. 2020, Chap. 13), where it forms two distinctive clades corresponding to summer and winter rainfall (Tolley et al. 2010). This species has long been known to have been introduced to St. Helena ~200 years ago with the suggestion that it was imported as duck food (Basilewsky 1970). Little information exists about the extent and impacts of this invasive population, except that it is still present today (N. Terblanche pers. comm.).

27.4.4 Reptiles

27.4.4.1 The Nile Monitor, *Varanus niloticus*

The introduction of the Nile Monitor to Florida, USA, dates back to at least 1990 (Campbell 2003; Enge et al. 2004), and now occupies an estimated area of ~50 km² of the freshwater canals, lakes and wetlands of Cape Coral (Campbell 2003). These animals were introduced through the pet trade, and likely released when they outgrew their owners (Enge et al. 2004). Impacts are anecdotal, but include predation on rabbits, goldfish and potentially feral cats (Campbell 2003). Stomach contents revealed aquatic and terrestrial vertebrates and invertebrates, including clutches of reptile and bird eggs and an adult Florida Burrowing Owl, *Athene cunicularia* (Campbell 2005). It is estimated that the population is in excess of 1000 individuals, and expanding onto nearby islands and along the coast (Campbell 2005).

27.4.4.2 The Tropical House Gecko, *Hemidactylus mabouia*

The Tropical House Gecko is endemic to a large part of central and East Africa, and its distribution extends into the northeast of South Africa. Kluge (1969) notes that the first record of *H. mabouia* outside Africa is in the Lesser Antilles in 1654. The distribution of invasive populations of Tropical House Geckos has recently been reviewed (Weterings and Vetter 2017), and includes much of South America, the Caribbean and North America, as well as scattered tropical islands. It is noteworthy that this species is successfully established outside of its native range within South Africa, another domestic exotic (see Measey et al. 2020, Chap. 5). It is still unknown whether any of the invasive populations originate from South Africa, or elsewhere in their distribution, although it seems plausible that some populations may have originated from South African ports such as Durban. Genetic analyses of populations in Florida (with samples from South America and Africa) suggest that it is unlikely that these introductions resulted from multiple source localities in Africa (Short and Petren 2011), instead suggesting that South America has acted as a bridgehead for other Caribbean and North American invasions. House geckos, and their eggs, are accidentally distributed by humans, having been moved long distances by cars (Norval et al. 2012). In their invaded range, they have been found to have near total overlap with other geckos exploiting the same anthropogenic niche (e.g. Short and Petren 2012).

27.4.4.3 Cape Dwarf Chameleon, *Bradypodion pumilum*

The Cape Dwarf Chameleon is restricted to a small area in the extreme southwest of Africa, where it inhabits both forest and fynbos habitats, although it has successfully moved into periurban areas around Cape Town and Stellenbosch, including

vineyards (Tolley and Burger 2012; Tolley and Measey 2007) where it is considered Near Threatened by the IUCN. Established populations were recorded in periurban gardens of Walvis Bay and Swakopmund in Namibia, and are presumed to have been deliberately introduced from gardens around Cape Town (Griffin 2000). These Walvis Bay populations were still present in 2004 (Bethune et al. 2004), but it could not be ascertained whether these populations, or another introduction to Luderitz (Griffin 2000) are extant.

27.4.5 *Fish*

27.4.5.1 Indo-Pacific Lionfish, *Pterois volitans* and *P. miles*

Although lionfish invasions were first ascribed to the Red Lionfish, *Pterois volitans*, genetic studies revealed a co-invasion by the Devil Firefish *P. miles* (Freshwater et al. 2009). As these species are difficult to distinguish in the field, most studies simply consider them as a single Indo-Pacific Lionfish invasion. Native to the Indo-Pacific region, including the East coast of South Africa, these were the first non-native marine fishes to establish in the Western North Atlantic (Schofield 2009). Although sporadic sightings were made for a decade before, it was only after 2000 that Lionfish increased in abundance and spread within the Western North Atlantic (Schofield 2009). Presently, invasions are recognised from the Caribbean Sea, the USA, the Mediterranean Sea, Netherlands and Venezuela (Schofield 2009, 2010; World Registry of Marine Species 2019). The invasion of the USA and ultimately the Caribbean is thought to be linked to the release of six individuals from an aquarium in south Florida when it was damaged during Hurricane Andrew in 1992 (Courtenay 1995). These invasive predators alter coral-reef ecosystems through predation of invertebrates and native fishes and competition with native predators. In fact, studies have demonstrated a decline of almost 80% in native fish recruitment in the presence of Lionfish (Albins and Hixon 2008).

27.4.5.2 Chubbyhead Barb, *Enteromius anoplus*

The Chubbyhead Barb is a resident in most catchments in South Africa (but absent from arid northwestern areas: from the Berg and Breede Rivers as well as the coastal rivers of the south-west and south Cape and the lower Orange River), and southern Mozambique (Skelton 2001). This species is thought to have been introduced to the Kuiseb system in central coastal Namibia (de Moor and Bruton 1988; Bethune et al. 2004). Dixon and Blom (1974) suggested that populations were introduced to the river pools of the Gaub (part of the Kuiseb system) by local farmers with stocks from the Orange or Olifants River in the South African Cape. Records show that *E. anoplus* was established in the late 1960s, but the current status of this population

is unknown. It is also possible that this population is not alien but that this isolated Namibian population is part of its natural range (P. Skelton pers. comm.).

27.4.5.3 African Sharp Toothed Catfish, *Clarias gariepinus*

Clarias gariepinus (Sharptooth catfish) is native to most of Africa and some parts of western Asia (Lebanon, Israel, and Turkey) (Skelton 2001). It is one of the most widely distributed fish on the African continent, with a native range that extends from the Nile in the north to as far south as the Orange system in South Africa. It has been introduced widely around the world, mainly to countries in Asia and a few countries in Africa, Europe, and South America (CABI 2019; Froese and Pauly 2019). The origin of most global introductions are not well documented, but include African countries, bridgehead introductions from Europe to Asia, and Asian countries (Froese and Pauly 2019).

Most introductions of the African Sharp Toothed Catfish have been for aquaculture, with some introductions facilitated by inter basin-transfer schemes and by direct stocking (Weyl et al. 2016, 2020, Chap. 6; Faulkner et al. 2020, Chap. 12, Box 22.2). The species is well suited for aquaculture because it can tolerate extreme environmental conditions such as low oxygen, high turbidity and desiccation (Donnelly 1973; Bruton 1979a). It also has favourable life-history traits such as early maturity, fast growth rate and good food conversion ratios (Na-Nakorn and Brummett 2009). These life history traits have also predisposed it to successful establishment in areas of introduction (Weyl et al. 2016).

Clarias gariepinus has a wide variety of prey that includes algae, macrophytes, invertebrates and vertebrates (Bruton 1979b). This wide trophic niche also implies that it can cause strong alterations at multiple trophic levels of invaded ecosystems through mechanisms such as predation and herbivory/grazing (e.g. Cambray et al. 2003; Vitule et al. 2006; Kadye and Booth 2012; Alexander et al. 2014).

27.4.5.4 Mozambique Tilapia, *Oreochromis mossambicus*

Oreochromis mossambicus (Mozambique Tilapia) is native to east flowing rivers in central and southern Africa. Its natural range extends from the lower Zambezi system in Mozambique to the Bushmans system in South Africa, extending far inland within the Limpopo River Basin, but south of the Pongola River system, it is naturally confined to coastal areas (Skelton 2001). The provenance of populations in Namibia is unknown (Dixon and Blom 1974). *Oreochromis mossambicus* is regarded as one of the most widely introduced fish species globally, and has been reported to have been introduced and is present in over 50 countries (Pullin et al. 1997; Froese and Pauly 2019). Early introduction records of *O. mossambicus* indicate that it was first introduced to the island of Java in Indonesia prior to 1930. Subsequent introductions have occurred all over the world mainly as bridgehead invasions from initial areas of

introductions (see Sect. 27.3.5). A large proportion of these introductions occurred within countries in Asia and Central America and the Caribbean.

Mozambique Tilapia has been widely distributed around the world for aquaculture and biological control of aquatic insects and macrophytes (Pullin et al. 1997; Froese and Pauly 2019). It is well-suited for aquaculture because it is easy to breed in captivity and it can tolerate a wide range of environmental conditions (Philippart and Ruwet 1982; Trewavas 1983). These adaptive life history characteristics have enabled it to occupy many different tropical and sub-tropical freshwater and estuarine niches in areas of introduction (Pullin et al. 1997). However, since the mid-1980s, there was a shift in producer preferences away from the *O. mossambicus* towards culturing of *O. niloticus* (Nile tilapia), which has a higher growth rate and reduced tendency to stunt (Pullin 1988).

Oreochromis mossambicus has been implicated in causing adverse environmental effects in areas of introduction (Canonico et al. 2005; Russell et al. 2012). Examples include competitive displacement of native species (e.g., Pérez et al. 2006), habitat alteration through herbivory (e.g., Doupé et al. 2010) and predation (de Silva et al. 1984). Despite these negative environmental effects, the introduction of *O. mossambicus* has in some cases (e.g. in Sri Lanka, Indonesia and Philippines), led to pronounced fisheries production and poverty alleviation by creating alternative aquaculture and fisheries livelihoods (de Silva et al. 2004). Although Mozambique Tilapia is considered invasive in most areas of introduction, in its natural range it is considered Endangered due to hybridisation with another introduced tilapia, *O. niloticus* (Firmat et al. 2013).

27.4.6 Invertebrates

Picker and Griffiths (2011) listed both the Big-headed Ant, *Pheidole megacephala*, and the Four-tone Nudibranch, *Godiva quadricolor*, as native to South Africa. However, other workers suggest that *P. megacephala* was originally from Cameroon or the northern part of sub-Saharan Africa. Wheeler (1922) concluded: “*In all probability Pheidole megacephala is of Ethiopian or Malagasy origin, as it shows a great development of subspecies and varieties in these two regions and nowhere else.*” Wetterer (2012), could find no subsequent study that questions this conclusion, including a genetic study by Moreau (2008) which suggested that it was most closely related to species from Madagascar and Ghana. Slingsby (2017) lists this species as being invasive in southern Africa (see Janion-Scheepers and Griffiths 2020, Chap. 7). Today, *P. megacephala* is present throughout South Africa, and it seems likely that South African invasions have played a bridgehead effect in the distribution of this species through some of its invasive range, as has been seen with other invertebrates (see Sect. 27.3.3.1). Similarly, Cervera et al. (2010) note that *G. quadricolor* rarely occurs outside of the Indo-Pacific, suggesting that although this species was first described from temperate False Bay in south-western South Africa, it is more likely to represent an early invasion.

27.4.6.1 The Geranium Bronze Butterfly, *Cacyreus marshalli*

The Geranium Bronze Butterfly, *Cacyreus marshalli*, is invasive in eastern Spain and the Mediterranean islands of Ibiza, Majorca and Menorca (Sarto i Monteyes 1992). This species appears to be spreading rapidly in Europe: Crete (Anastassiou et al. 2010), Capania (northern Italy: Pignataro et al. 2006), the Balkan peninsula (Marko and Verovnik 2009), Republic of Northern Macedonia (Micevski and Micevski 2017) and in Egypt (Fric et al. 2014). Moreover, the risk of further spread of this species in Europe has been suggested, together with economic impacts to the horticultural trade, particularly against geraniums and pelargoniums (Quacchia et al. 2008). Sightings of this species have now been made throughout the Canary Islands and on Reunion (iNaturalist, accessed May 2019).

27.4.6.2 South African Mantis, *Miomantis caffra*

This praying mantis was first recorded in Auckland, New Zealand in 1978 (Ramsay 1990), from where it has spread throughout North Island, Nelson, and has recently been found in Christchurch (Fea et al. 2013). There is speculation that this species was introduced and has been moved around by accidental transport of the ootheca (egg masses), which can be adhered to crates. Brockerhoff et al. (2010) suggested that this mantis is a predator of native invertebrates and may compete directly with the native New Zealand mantis, *Orthodera novaezealandiae*, which is now thought to be in decline as *M. caffra* is more aggressive, longer lived, and has more offspring (Ramsay 1990; Buckley et al. 2014). Moreover, native male *O. novaezealandiae* are more attracted to the scent of the invading *M. caffra* which respond by preying on the natives (Fea et al. 2014). Marabuto (2014) recorded this same mantis from Vila Sol, Faro, in the south of Portugal in August 2014. It is not known whether this is a second invasion from southern Africa or a secondary invasion from New Zealand. Records on iNaturalist (accessed May 2019) suggests that *M. caffra* has recently established in both Sydney and Melbourne, Australia.

27.4.6.3 Brown Widow Spider, *Latrodectus geometricus*

The Brown Widow Spider is distributed globally, with known invasive populations in North and South America, Hawaii and across Australasia. The small amount of genetic diversity globally, and the sister taxon being the southern African *L. rhodesianus* suggest a recent expansion from Africa (Garb et al. 2004), although it is not known whether the South American distribution has been anthropogenically facilitated. The distinctive spikey egg sacs adhere to outdoor objects (such as plant pots), and therefore are easily transported accidentally. Currently, it is not understood whether known invasive populations were introductions from South Africa. Bites from this spider can be medically important, although most cases appear not to

warrant medical attention (Müller 1993). Within its invasive distribution, this species is strongly associated with domestic habitats in peri-urban environments (Vetter et al. 2012b), which means that it often comes into contact with people and therefore has a high chance of being moved around. There are reports that Brown Widows displace Black Widows, *L. hesperus* (Bianchi 1945; Baerg 1954), although this displacement may not be through competition but from enemy release from egg predation and parasitism (Vetter et al. 2012a). As the former bite less frequently and are less toxic it is thought that this displacement is of benefit to people (Vetter et al. 2012b).

27.4.6.4 Brown Mussel, *Perna perna*

Although originally described with a wider native distribution, the intertidal mussel *Perna perna* is now accepted as naturally occurring along the coasts of South Africa, Namibia, Angola, Mozambique, Madagascar and India (Berry 1978; Souza et al. 2003). While there has been some contention about its status in Brazil, the absence of shells from hunter-gatherer middens is now accepted as evidence that this mussel is not native to South America (Souza et al. 2003). This mussel is also alien in the Mediterranean Sea having arrived sometime before the 1970s (Berry 1978; Ahyong et al. 2019). Most recently, *P. perna* has invaded the Caribbean and the Gulf of Mexico (Hicks and Tunnell 1993). It is likely that shipping is the pathway of introduction for this species (Hicks et al. 2001), with hull fouling the likely vector. Although the ecological impacts of this mussel have not been quantified in its invaded range these mussels act as ecosystem engineers, offering habitat and protection to infaunal biota on the South Africa shoreline (Hammond and Griffiths 2006). Thus, if the mussel becomes dominant in an area that previously supported few mussels it could increase abundance and diversity of associated infauna (Sadchatheeswaran et al. 2015). Economic impacts have been associated with the invasion in the Gulf of Mexico where the species is considered to pose a risk to shipping safety as it can sink navigation buoys (Hicks and Tunnell 1995). It is also known to colonise jetties, petroleum platforms, wrecks and other artificial hard substrata (Hicks and Tunnell 1995). While this species can bring with it economic benefits from culturing (Ferreira et al. 2006), it concurrently poses a threat to human health as it can be affected by paralytic shellfish poisoning (Barbera-Sanchez et al. 2004).

27.4.6.5 Shell-Boring Polychaete, *Terebrasabella heterouncinata*

This marine tube-dwelling worm originates from the coast of South Africa (Fitzhugh and Rouse 1999). It was noted in California in 1993 after being unintentionally imported along with South African abalone (Kuris and Culver 1999). It has since spread to Mexico and Chile (Kuris and Culver 1999; Moreno et al. 2006). *Terebrasabella heterouncinata* is considered a pest as it causes shell abnormalities when boring into commercially important abalone (Fitzhugh and Rouse 1999). It

escaped into the wild at one site in California, infecting native gastropods in high numbers (Culver and Kuris 2004). However, an intensive and prolonged management programme saw this aggressive invader extirpated from this location (Culver and Kuris 2000) and its prevalence reduced in farms.

27.4.6.6 Spionid Worm, *Boccardia pseudonatrix*

A native to the South African coast (Simon et al. 2010), this shell-boring polychaete has spread to Australia, New Zealand and Japan (Walker 2014; Abe et al. 2019). While *B. pseudonatrix* was first reported on farmed oysters in Australia in 2014, examination of preserved specimens revealed its earlier presence in New Zealand. As oysters have never been imported to Australia from South Africa, it is thought that the Australian occurrence represents natural spread from the introduced range in New Zealand (Walker 2014). The pathway of introduction to Japan is yet to be established. Although the impacts of this species have not been explicitly measured in its introduced range, the fact that this species impacts oyster and abalone culture and infests wild oysters in South Africa (Simon et al. 2010; Boonzaaier et al. 2014) suggests that it is likely to have similar consequences in its introduced range.

27.5 Conclusions

Compared to the large number of alien plant species originating from South Africa (Pyšek et al. 2020, Chap. 26), the number of alien animals has been small. If, as we speculate, the hiatus in trade relations between South Africa and the rest of the world led to the low number of donations recorded here, it could be that there is a significant invasion debt (Rouget et al. 2016). We suggest that candidate species which could be added to watch lists are those that are already domestic exotics within South Africa. South Africa also plays an important role in bridgehead effects, and this could be set to increase if it continues to act as a major commercial hub, especially for alien pets.

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