

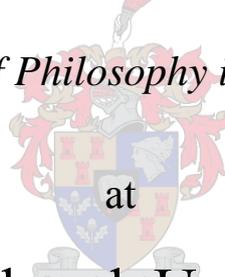
The extent, impact and management of ungulate translocations

by

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Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the owner of the copyright thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: 17 November 2008

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Abstract

The worldwide movement of biota is of substantial concern for the conservation of biodiversity. The movement of species takes place at three different scales. These are translocations of indigenous species within their natural distribution ranges, the translocation of species outside their natural distribution ranges within geopolitical boundaries (i.e. extralimital introductions) and the translocation of species outside geopolitical boundaries and their natural distribution ranges (i.e. extraregional introductions). Ungulates are extensively translocated at each of these scales and each scale of translocation is expected to have different impacts on biodiversity. Ungulates are translocated for conservation purposes such as reintroducing species to places where they have previously gone extinct and to mitigate inbreeding in small, isolated populations. Ungulates are also extensively translocated for economic and recreational reasons, such as for sport hunting. Translocations for sport hunting include indigenous, extralimital and extraregional species. Concerns for translocations of indigenous species are largely for the loss of genetic diversity through the mixing of genetically distinct populations, and concerns for extralimital and extraregional translocations are for impacts on indigenous biodiversity such as through herbivory, competition, hybridization and disease transmission. This thesis investigates the extent of ungulate introductions globally and at a finer resolution in South Africa. It investigates the pathways, drivers and impacts of ungulate introductions and it also investigates the use of surrogates for genetic distinctiveness for advising the translocation of indigenous ungulates. The study finds that ungulate translocations have been extensive and have led to the homogenization of ungulate assemblages in countries globally and at a quarter-degree grid-cell resolution in South Africa. Zoos were identified as a potential introduction pathway for extraregional ungulates globally and in South Africa extraregional introductions have made ungulate assemblages more different; whereas large numbers of extralimital introductions have made ungulate assemblages more similar. The homogenization of ungulate species in South Africa has increased with time, due to increased numbers of translocations, particularly of extralimital species. In South Africa translocations have most recently been made to high-income areas with high human population density and high livestock density; whereas in the 1960s ungulates were introduced to areas species

poor for indigenous ungulates and marginal for livestock. In South Africa, long distance translocations of indigenous species extralimitally has resulted in extensive range expansions of a magnitude greater than predicted range changes as a result of predicted climate change. When the use of surrogates of genetic distinctiveness for advising translocations was investigated for Africa, the East African rift valley was found to be important in delineating genetic distinctiveness and translocations across this feature should be prevented. Major rivers in Africa also showed potential for delineating genetic distinctiveness in ungulates, but relevant phylogeographic data are needed to confirm this. Sufficient evidence for the impacts of non-indigenous ungulates on biodiversity both in South Africa and globally is lacking despite substantial concern for their impacts. It is suggested that to demonstrate the impacts of non-indigenous ungulates exclosure and enclosure experiments should be used and population declines in indigenous species should be shown.

Opsomming

Verskuiwing van plante en diere wêreldwyd lei tot groot kommer in gevolge die bewaring van biodiversiteit. Verskuiwings vind op drie skale plaas, naamlik, die verskuiwing van inheemse spesies binne hulle natuurlike verspreidingsgebied, die verskuiwing van spesies buite hul natuurlike verspreidingsgebied maar binne landsgrense (d.w.s. buite limiet verskuiwings), en die verskuiwing van spesies buite hul natuurlike verspreidingsgebied en buite landsgrense (d.w.s. buite grondgebied verskuiwings). Grootskaalse verskuiwing van hoefdiere vind op al drie skale plaas. Verskuiwing op elk van die skale sal na verwagting biodiversiteit verskillend beïnvloed. Hoefdiere word ook vir bewaringsdoeleindes verskuif, bv. die herbevolking van 'n gebied waar die spesies uitgesterf het, asook om genetiese probleme wat gepaardgaan met klein bevolkingsgroottes te vermy. Hoefdiere word ook verskuif vir ekonomiese- en ontspannings redes, o.a. vir sportjag, en sluit verskuiwings op al drie skale in. Kommer oor verskuiwings binne 'n spesies se verspreidingsgebied rus hoofsaaklik op die verlies van genetiese diversiteit a.g.v. die vermenging van vorig genetiese eiensoortige bevolkings, terwyl op die ander twee skale kommer hoofsaaklik gebaseer is op die impakte van kompetisie, interteeling, predasie, herbivoor effek, en die verspreiding van parasiete op inheemse biodiversiteit. Hierdie proefskrif ondersoek die omvang van hoefdier verskuiwings globaal asook in Suid Afrika. Die verskuiwingsweë, oorsake en impakte van verskuiwings word hier ondersoek, asook die maatstawwe van genetiese eiensoortigheid om advies oor verskuiwings te verskaf. Die bevindings toon op ekstensiewe verskuiwing van hoefdiere wat eenvormigheid van hoefdier spesiesamestellings wêreldwyd bevorder het, sowel as op 'n kwartgraad skaal in Suid Afrika. Dieretuine is geïdentifiseer as 'n potensiële bron van buite grondgebied verskuiwings. In Suid Afrika het buite grondgebied verskuiwings hoefdier spesiesamestellings minder eenvormig gemaak, terwyl buite limiet verskuiwings hoefdier samestellings binne Suid Afrika meer eenvormig gemaak het. Eenvormigheid in hoefdier spesiesamestellings het met tyd in Suid Afrika toegeneem as gevolg van 'n toename in veral buite limiet verskuiwings. In Suid Afrika is verskuiwings mees onlangs na hoë-inkomste gebiede met hoë menslike bevolkings- en veëdigthede gemaak. In die sestiger jare is hoefdiere egter verskuif na gebiede

waar min inheemse hoëdiere voorgekom het en wat marginaal was vir veëboerdery. In Suid Afrika het langafstand buite limiet verskuiwings versoorzaak dat die verspreidingsgebiede van sekere hoëdier spesies groter is as wat die geval sal wees met voorspelde klimaatsveranderinge. Wanneer surogaat inligting gebruik word om genetiese verskille tussen bevolkings te identifiseer om verskuiwings te adviseer, word die Oos Afrika Rift vallei geïdentifiseer as 'n belangrike breuk tussen bevolkings. Verskuiwings oor die vallei moet verkieslik nie plaasvind nie. Groot riviere in Afrika speel 'n soortgelyke rol, maar verdere genetiese inligting is nodig om dit te bevestig. Alhoewel kommer oor die impak van verskuiwings groot en teoreties verdedigbaar is, bestaan daar te min konkrete bewyse vir die impakte in Suid Afrika. Daar word voorgestel dat manipuleringseksperimente uitgevoer moet word om impakte te demonstreer, en dat aandag veral gegee moet word aan die demonstrasie van impakte op inheemse spesies.

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- Chapter I -

Introduction

The worldwide movement of biota is a substantial concern for the conservation of biodiversity (Elton, 1958; Vitousek *et al.*, 1996) and it occurs at three main scales. Indigenous species are translocated within their 'historical' distribution ranges with implications for the transfer of pathogens and parasites (Braack *et al.*, 1995) and the loss of genetic diversity if genetically distinct populations are mixed (Storfer, 1999). Species are translocated outside their 'historical' distribution ranges but within geopolitical or biogeographic boundaries (extralimital introductions) and species are translocated outside geopolitical or biogeographic boundaries and their 'historical' distribution ranges (extraregional introductions). Extralimital or extraregional species that establish and spread are known as invasive species (see Williamson, 1996; Richardson *et al.*, 2000) and are recognized as one of the most serious threats to biodiversity globally (Wilcove *et al.*, 1998; Chapin *et al.*, 2000). They alter the composition of species assemblages (Olden *et al.*, 2004) and may negatively impact indigenous biodiversity (Mack *et al.*, 2000; Mooney & Cleland, 2001).

Biological invasions and their impacts

Different taxa are translocated for different purposes, such as agriculture (Diamond, 1998; Pimentel, 2002), conservation and recreation (Griffith, 1989), and are translocated via different pathways (Hulme *et al.*, 2008). Plants and invertebrates are often introduced accidentally, although many species have been intentionally introduced for economic reasons (Pimentel *et al.*, 2000; Mack & Erneberg, 2002). Extensive translocations of species, such as of food crops have lead to some species having ubiquitous distributions. For example, cereal crops, which originated in the fertile crescent *c.* 9000 years ago now have global distributions (Diamond, 1998) and *c.* 90 % of the worlds' food is produced by 15 plant species that are now distributed worldwide (Pimentel, 2002).

Vertebrates are often intentionally introduced for food and as game (Lever, 1985; Kraus, 2003) and vertebrate translocations may have been occurring since the

Pleistocene (White, 2004). The trading of caged birds goes back to the time of the spice trade and one of the oldest hypothesised mammalian translocations is that of a marsupial 20 000 years ago (Heinsohn, 2001). The trading of animals remains an important pathway for the introduction of vertebrates. For example, the pet trade for reptiles (Brown, 2006) and birds (Cassey *et al.*, 2004), and the aquaria trade for fish (Arndt *et al.*, 2002; Padilla & Williams, 2004; Semmens *et al.*, 2004; Rixon *et al.*, 2005; Weigle *et al.*, 2005). Translocations such as these are likely to increase with increasing global trade (Levine & D'Antonio, 2003; Westphal *et al.*, 2008). Once introduced vertebrates are likely to establish and spread (Jeschke & Strayer, 2005) and establishment success is expected to be greatest under conditions of high propagule pressure (i.e. the number of individuals introduced at each introduction event and the number of introduction events) (Lockwood *et al.*, 2005). Indeed propagule pressure has been important in the establishment success of birds and mammals in New Zealand (Forsyth & Duncan, 2001) and Australia (Duncan *et al.*, 2001; Forsyth *et al.*, 2004).

Recent investigations into the distribution of non-indigenous species, mostly in the United States, have shown that larger numbers of non-indigenous species are often found in areas with high indigenous species richness (plants - McKinney, 2001, 2006; Stohlgren *et al.*, 2003, 2006, birds - McKinney, 2006; Stohlgren *et al.*, 2006, and mammals and herptiles - McKinney, 2006). Fish are an exception, and in the United States more non-indigenous fish are found in areas that are species poor for indigenous fish species (McKinney, 2001; Stohlgren *et al.*, 2006). This has been attributed to fish being introduced by the game agency to increase species available for fishing (McKinney, 2001). The relationship between indigenous and non-indigenous species is not recognised as being one of cause and effect (Stohlgren *et al.*, 2003). More non-indigenous species are also found in places with high human population densities (plants - McKinney, 2001, mammals and herptiles - McKinney, 2006), which tend to be productive areas that are of high indigenous species richness (Chown *et al.*, 2003; Araújo, 2003; Stohlgren *et al.*, 2006). Humans also facilitate the establishment of non-indigenous species in these areas (McKinney, 2006; Stohlgren *et al.*, 2006).

Non-indigenous species impact ecosystems through direct and indirect influences on indigenous species and abiotic processes, and may cause extinctions (Mack *et al.*, 2000; Mooney & Cleland, 2001; White *et al.*, 2006). They “eat indigenous species, change their habitat, compete with them, hybridize with them and infect them” (Simberloff *et al.*, 2005). Indeed the literature on species that have had serious impacts on biodiversity is steadily growing (see Mack *et al.*, 2000). For example, predation often leads to extinctions on islands, where mammals such as stoats, cats and rats have extirpated endemic birds (see Blackburn *et al.*, 2004), and introduced predatory fish have decimated endemic fish species in freshwater systems (Goldschmidt, 1996). Competitive exclusion has been demonstrated by the Argentine ant, *Linepithema humile*, which has displaced a number of indigenous ant species (Human & Gordon, 1996; Holway, 1999; Sanders *et al.*, 2003) and arthropods (Lach, 2007) worldwide, thereby altering assemblage structure and ecosystem functioning. Well known examples of the problem of hybridization between introduced and indigenous species include hybridization of the widely introduced Mallard duck, *Anas platyrhynchos*, with various endemic duck species leading to introgression in the New Zealand grey duck, *Anas superciliosa* (Rhymer *et al.*, 1994), and hybridization and introgression of introduced trout with endemic fish (Echelle & Echelle, 1997). New evidence for introduced fish forming a hybridization bridge between indigenous species has also come to light (McDonald *et al.*, 2008). An example of introduced species infecting indigenous ones comes from the importation of nursery plants that introduced Asian chestnut blight fungus, which went on to destroy billions of American chestnuts, *Castanea denata* (Roane *et al.*, 1986). Invasive species not only influence single species but have substantial impacts on entire ecosystems (Vitousek, 1990). For example, the non-indigenous crazy ant, *Anoplolepis gracilipes*, has impacted at least three trophic levels in a rain forest ecosystem and has influenced ecosystem processes (O’Dowd *et al.*, 2003), and the Australian paperbark tree, *Melaleuca quinquenervia*, has invaded Florida forming dense stands, replacing indigenous vegetation, altering habitats, using large amounts of water, and altering fire regimes (Schmitz *et al.*, 1997).

A natural experiment of the consequences of introduced species comes from continental interchanges of species. The best documented of these is the great American interchange which occurred after the connection of South and North

America c. 3 million years ago by the Panama land bridge (Marshall, 1988). While South American mammalian faunas had been evolving in isolation and were mostly endemic, North American faunas had intermittent links with Europe and Asia and had experienced previous interchanges with these continents (Marshall, 1988). It has been hypothesised that, after connection by the land bridge, invading North American ungulates replaced many South American ungulates by out-competing them (Simpson, 1950; Webb, 1976) and that the process was facilitated by novel predators to which South American ungulates were naïve (Webb, 1976). This theory has been debated a great deal and more certainty and support has been gained for the idea that North American marsupial carnivores replaced those in South America (Webb, 1991, Vermeij, 1991).

Biotic homogenization

The introduction and establishment of new species, often the same species, around the world has resulted in biotas becoming more similar globally (McKinney & Lockwood, 1999). This process of replacing distinct local species assemblages with more cosmopolitan non-indigenous ones is known as homogenization and is a result of the introduction of non-indigenous species and the extinction of indigenous species (McKinney & Lockwood, 1999). The impacts of homogenization differ from invasion by single species in that homogenization reduces resistance to environmental change, simplifies foodwebs and increases susceptibility to further invasions (Olden *et al.*, 2004). Homogenization leads to the loss of distinctiveness of functionality, taxonomy and genetic variation in communities (Olden *et al.*, 2004). Functional homogenization is the reduction of functional diversity in a community e.g. replacing specialists with generalists (Olden *et al.*, 2004). Taxonomic homogenization reduces the spatial component of variation in species assemblages as explained above and “*genetic homogenization reduces the spatial component of genetic variability within a species*” (Olden *et al.*, 2004).

The investigation of the homogenization of biotas is relatively new and Olden (2006) recently outlined the areas of investigation that should be prioritized. Some of his suggestions include the investigation of homogenization at multiple spatial and temporal scales, focusing on invasions and extinctions, and the environmental drivers involved (Olden, 2006). To date the majority of homogenization studies have focused

on plants (Rejmánek, 2000; McKinney, 2004, 2005) and fish (Rahel, 2000; Taylor, 2004) in North America. These studies have shown that although biotas have become substantially more similar through the introduction of the same species to various places, in some cases species assemblages have become more different (e.g. Marchetti *et al.*, 2001). Most often biotas in close proximity have become more different as a result of different species being introduced to localities with similar species assemblages (Olden & Poff, 2003; Qian & Ricklefs, 2006).

Ungulate translocations

Ungulates have been moved around since historic times for food and hunting (Lever, 1985). Rusa deer, *Rusa timorensis*, were most likely introduced to the Melanesian islands and Sulawesi *c.* 5000 years ago for food and hunting (Heinsohn, 2001). As early as *c.* 9000 years ago cattle were translocated to provide a reliable food source to areas where wild antelope and deer numbers had been reduced (Diamond, 1998) and in the 1660s, Charles II of England satisfied his hunting interests by translocating deer (Graham, 1973). In the last century the introduction of ungulates for hunting has been particularly common and these species currently bring in substantial economic revenue from hunting (Hofer, 2002; Lindsey *et al.*, 2007). Countries which have introduced ungulates for sport hunting include Argentina (Godoy, 1963 in Veblen *et al.*, 1989; Veblen *et al.*, 1992), Australia (Lever, 1985), Chile (Jaksic *et al.*, 2002), Kenya (Graham, 1973), New Zealand (Forsyth & Duncan, 2001), South Africa (Brooke *et al.*, 1986), Spain (Cassinello, 1998), Tunisia (Lever, 1985) and the United States of America (Mungall & Sheffield, 1994).

Globally there is concern about the impacts that introduced ungulates are having on biodiversity (e.g. Brooke *et al.*, 1986; Demarais *et al.*, 1990). Like other invasive species, ungulates alter habitat and the functioning of ecosystems (Wardle *et al.*, 2001) and they compete with (Baccus *et al.*, 1985; Côté, 2005), eat (Fordham *et al.*, 2006), infect (Meltzer, 1993) and hybridize with (Goodman *et al.*, 1999) indigenous species. The potential negative impacts of non-indigenous ungulates on biodiversity and their economic importance have led to competing interests regarding their management (see Veblen *et al.*, 1992; Castley *et al.*, 2001; Bradshaw *et al.*, 2007), and it is becoming increasingly important to convince landowners of the impacts of non-indigenous ungulates, so that they will be more willing to comply with ungulate

management regulations (see Bradshaw *et al.*, 2007). Knowledge of the impacts of non-indigenous ungulates is also required for assessing the risks of ungulate introductions.

Non-indigenous ungulate translocations for hunting are not the only translocations that are of concern. Indigenous species are often translocated within their 'historical' distribution ranges and the implications of such translocations for genetic variation are particularly concerning (Greig, 1979; Randi, 2005). Genetic diversity is fundamentally important for the persistence of species, especially in the face of global change (Lacy *et al.*, 1997) and it is well known that genetic distinctiveness often increases with geographic distance between populations (Slatkin, 1993) due to vicariance, isolation and reduced gene flow. Therefore the mixing of distant populations could lead to the loss of genetic diversity (Storfer, 1999). The translocation of ungulate species within their distribution ranges is extensive for hunting (Griffith, 1989), but also occurs for restocking of protected areas (Penzhorn, 1971; Polziehn *et al.*, 2000; Lee *et al.*, 1994). On a large scale, these translocations could lead to genetic homogenization (see Olden *et al.*, 2004). In the United States, white-tailed deer, *Odocoileus virginianus*, has been reintroduced to national parks and genetic analyses have shown that populations that have received translocated individuals are more similar to the source populations of translocated individuals (DeYoung *et al.*, 2003). Endangered species such as black rhino, *Diceros bicornis*, have been translocated large distances across Africa in the past to restock populations (e.g. Penzhorn, 1971), but it has been advised, instead, to translocate individuals from populations in close proximity, that are likely to be genetically more similar (Swart & Ferguson, 1997). However, to prevent genetic introgression it is vital to know which populations are genetically distinct (Riddle & Jones, 1996) so that translocations between these populations can be prevented, but this information is seldom available (Namkoong, 1996).

Ungulate translocations in South Africa

South Africa has a substantial history of ungulate introductions (Bigalke & Bateman, 1962; Siegfried, 1962; van Ee, 1962; Chapman & Chapman, 1980; Lloyd & Millar, 1983; Smithers, 1983; Brooke *et al.*, 1986) and translocations of indigenous species within and outside their 'historical' ranges (du Plessis, 1969; Lambrechts, 1974;

Lloyd & Millar, 1983; Howard & Marchant, 1984; Brooke *et al.*, 1986). Translocations in South Africa have been undertaken for hunting and eco-tourism (Castley *et al.*, 2001) and to restock national parks where species have been extirpated due to hunting and land-use change due to agriculture (Penzhorn, 1971). Concern regarding the loss of genetic diversity in ungulates in South Africa has been expressed by Greig (1979) and concern for their impacts on biodiversity by Brooke *et al.* (1986). South Africa enacted the National Environmental Management: Biodiversity Act (Anonymous, 2004), which has been recently updated (Anonymous, 2007). This Act restricts the introduction of non-indigenous species and also limits the movement of ungulate species between designated population boundaries (Anonymous, 2007). These regulations have met substantial resistance from the hunting industry due to their financial implications (S.L. Chown, personal communication).

Due to the accessibility of relevant data, South Africa provides a useful case study for the investigation of taxonomic homogenization in ungulates, the drivers of ungulate introductions, pathways of introduction, propagule pressure and range change as a result of ungulate species being translocated extraliminally. The investigation of the impacts of non-indigenous ungulates on biodiversity and insight into the management of translocations within indigenous species ranges are especially pertinent to South Africa due to the conflicting views of conservation authorities and landowners with interests in non-indigenous ungulate species and ungulate species translocations. All of these lines of inquiry are further applicable to many other countries due to the prevalence of ungulate translocations for hunting globally.

The aims of this study are therefore to 1) assess taxonomic homogenization of ungulate species globally and locally in South Africa, including investigations into the pathways and drivers of ungulate introductions 2) investigate ungulate translocations in South Africa, analysing the distances species are translocated, the resultant extent of range change, and evidence of realised impacts of ungulate introductions in South Africa, 3) determine general principles to apply to the translocation of ungulate species in Africa, to limit the loss of genetic diversity, 4) examine the evidence for the realised impacts of non-indigenous ungulates on biodiversity and 5) develop recommendations for the translocation and introduction of ungulate species in South Africa based on the outcomes of this study.

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- Chapter II -

Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales

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INTRODUCTION

Anthropogenic, biotic homogenization is now recognized as an important problem for conservation. Regionally distinct, indigenous assemblages are being replaced with more cosmopolitan, non-indigenous ones, as a consequence of extinctions, the introduction of non-indigenous species, or some combination of the two (McKinney & Lockwood, 1999; Olden & Poff, 2004; Olden, 2006). Whilst biotic differentiation can also result from these processes (Olden & Poff, 2003), most studies have demonstrated the converse (Olden, 2006). Homogenization has impacts distinct from invasion by single species, including reducing resistance to environmental change, foodweb simplification, and increased susceptibility to further invasions (Olden *et al.*, 2004).

Despite its growing significance, many aspects of biotic homogenization remain poorly investigated. The range of taxa and the number of regions in which biotic homogenization has been explored are relatively small. Most work has focussed on taxonomic homogenization in plants or fish, predominantly in continental North America (e.g. Rahel, 2000; Rejmánek, 2000; McKinney, 2004a, 2005; Taylor, 2004), with investigations of homogenization at other levels and for other groups being less common (Lockwood *et al.*, 2000; Olden, 2006; Smith, 2006). The effects of spatial scale and autocorrelation on the extent of homogenization or differentiation have also been poorly documented (Taylor, 2004; Marchetti *et al.*, 2006; see also Nekola & White, 1999). For example, it has been predicted that at coarse spatial grains homogenization will be more pronounced than at finer grains, and that over short

distances biotic differentiation should be more common than homogenization (Olden & Poff, 2003; Olden, 2006).

Similarly, the underlying proximate causes of homogenization are incompletely known, although they are clearly intimately related to the causes of extinction and the mechanisms that result in the successful introduction and establishment of non-indigenous species (see e.g. Lawton & May, 1995; Duncan *et al.*, 2003; Sax & Gaines, 2003; Blackburn *et al.*, 2004; Lockwood *et al.*, 2005; Sax *et al.*, 2005; Light & Marchetti, 2007). These might include urbanization, human landscape alteration, climate change favouring introduced over indigenous species, interactions between indigenous and invasive species, and synergies between introduced species (Richardson *et al.*, 2000; Prinzing *et al.*, 2002; Stachowicz *et al.*, 2002; Goulson, 2003; McKinney, 2006a; Richardson & Pyšek, 2006; Chown *et al.*, 2007).

Likewise, the relationships between rates of introduction and extinction, changes in species richness, and changes in community similarity at the taxonomic level are not well understood, though a wide variety of predictions have been made (Olden & Poff, 2003). In this context, the contribution of introductions of species outside their natural geographic ranges within a given geopolitical (or biogeographic) area (i.e. extralimital introductions) relative to introductions from wholly outside the geopolitical area (extraregional introductions) is poorly known. McKinney (2005) found that extralimital introductions led to greater homogenization than extraregional introductions in fish and plants in the continental United States. Such extralimital introductions are surprisingly common; given the legislative frameworks within which introductions of non-indigenous species are regulated (United Nations, 1993; DEST, 1996; Clinton, 1999; Anonymous, 2004; Environment Canada, 2004). They also have considerable implications for genetic homogenization (see Olden *et al.*, 2004), especially in those regions with substantial spatially-structured genetic variation.

These gaps in current knowledge have been identified as ‘pressing research needs’ by Olden (2006), who called for further research efforts in this area. Recognizing that modern introductions of non-indigenous species constitute an unprecedented kind of environmental change (Cassey *et al.*, 2005; Ricciardi, 2007), this call is answered by investigating biotic homogenization in ungulates at the global level, and at the local

level within South Africa. Ungulates were chosen for several reasons. They have a substantial history of translocation for economic (including recreational) purposes and remain of considerable interest in this regard (Hofer, 2002; Long, 2003; Dryden & Craig-Smith, 2004; Lindsey *et al.*, 2007). They have also become the subject of contentious translocation proposals for ‘re-wilding’ (Donlan, 2005; Zimov, 2006), and the genetic consequences of translocations are also of serious concern (Allendorf *et al.*, 2001; Hartl *et al.*, 2003, Randi, 2005). Examination of homogenization at the global level, and the country level in South Africa, also provides substantial scope for understanding the contribution of scale to patterns of homogenization, and for understanding the proximate reasons for extralimital introductions (or translocations).

Specifically, in this study, I determine: 1) the patterns of taxonomic homogenization in ungulates for countries globally and in South Africa at three spatial resolutions; 2) how homogenization has changed over time in South Africa; 3) how homogenization differs with changes in species richness; 4) whether ungulate assemblages within a region are more likely to be homogenized by extralimital introductions than by extraregional introductions and; 5) whether extirpations within countries have contributed to homogenization and how this is likely to change if species that are currently considered to be endangered or in a higher IUCN threat category (IUCN, 2006) are considered extinct. Given that many ungulate introductions are intentional (Long 2003, but see Brooke *et al.*, 1986; Baker, 1990 for exceptions), I also briefly examine: 6) the pathways of introduction at the global scale and 7) proximate explanatory variables for ungulate introductions at the local scale within South Africa.

METHODS

Taxa, regions and data sources

By convention the ungulates are taken to include the orders Artiodactyla and Perissodactyla (following Wilson & Reeder, 2005), acknowledging that such a grouping is polyphyletic (e.g. Bininda-Emonds *et al.*, 2007).

At the global level, the study was conducted on a geopolitical basis (i.e. by country – for similar geopolitical approaches see Qian & Ricklefs (2006) and Olden (2006)) largely because data on introduced species are typically recorded in this way (Lever, 1985; Long, 2003). Species data for each country were obtained for indigenous

species from Wilson & Reeder (2005), and for established non-indigenous ungulates (EST) from Lever (1985) and Long (2003). Those indigenous species that have been extirpated (EXT) were also noted and data for endangered ungulates were obtained from the IUCN's (2006) red list of threatened species to represent those species that are likely to become extinct in the near future. In this variable, END, those species already extinct were also included.

At the local scale, the study focussed on South Africa (1 219 912 km²), a country rich in both indigenous (Wilson & Reeder, 2005) and non-indigenous (Brooke *et al.*, 1986; Castley *et al.*, 2001) ungulate species. Here, a quarter-degree grid-cell (~ 25 km x ~27 km = ~675 km²) resolution was used. These data were also concatenated to one-degree grid-cells (ODGC) (~100 km x ~108 km = ~10 800 km²) and two-degree grid-cells (TDGCs) (~200 km x ~216km = ~43 200 km²). Indigenous ungulate data were assigned to quarter-degree grid-cells (QDGCs) for a species if more than half of the grid-cell fell within the species extent of occurrence provided by Keith (2004). For ungulate introductions, the hunt and game sale advertisements in the classified section of the Afrikaans *Landbou Weekblad* (Farmer's Weekly) magazine were searched for all issues between 1965 and 2005. Hunt and sale advertisements were assumed to indicate the presence of an established population of the species in the specified area. That is, farmers were assumed to be advertising excess stock from an established population on their land. However, the absence of an advertisement does not indicate the absence of an established population and only QDGCs with advertisement data were included in analyses. This potential bias should be kept in mind throughout. Data from large auctions were specifically excluded because provenance of the species sold at auctions is less certain. Data collected included year, place and species. In the absence of place names the dialling code provided was recorded. Dialling codes were assigned to QDGCs using telephone directories dating back to the relevant time period. Less than 30% of the data was compiled using dialling codes. Dialling codes covered areas of c. 1 500km² (just over two QDGCs) for most of the study period, but by 2005 dialling codes covered areas of up to 30 000 km². In instances where the area covered by a dialling code included several places, data were assigned to a central QDGC. Advertisements listing mobile phone numbers were not used. The coordinates of places were obtained using a hierarchy of coordinate search websites: www.routes.co.za, www.fallingrain.com/world/SF and www.earthsearch.net. Data

were divided into species introduced from other regions in South Africa (extralimital) and species introductions from outside the country (extraregional). For validation, the *Landbou Weekblad* data were compared with introduction data obtained from other independent studies (see Table 1). There was congruence between species presence between data sets. Mean similarity in data between sites with data was 52% and overlap in data from the two sources was 39%.

To investigate the proximate explanatory variables for non-indigenous ungulate introductions at the local scale in South Africa, four predictors of the number of established introductions were examined at the QDGC scale: indigenous ungulate species richness, agricultural marginality, average annual income and human population density (Statistics South Africa, 1996). It was assumed that introductions to farms may be made to enhance the economic viability of the farm (more pronounced in agriculturally marginal areas, in areas with low average income, and possibly in low population density areas). Livestock data for 2005, specifically the total number of goats, cattle, sheep and pigs (Department of Agriculture, 2005) were used as a measure of marginality as was average annual income (Statistics South Africa, 2001). The agricultural production and human population density data are likely to have changed over the 40 years of analysis. However, good spatial data on both, stretching back to 1965, are not readily available (see Evans *et al.*, 2006 for data on human population density change for South Africa between 1996 and 2001).

Analyses

Homogenization was represented by the change in similarity between sites (countries or degree grid-cells) as a result of introductions, and for a second analysis as a result of both introductions and extinctions. Values of similarity were calculated using Jaccard's index of similarity (JI) i.e. the number of shared species divided by the total number of species between a pairwise comparison (Jaccard, 1912). Whilst other estimates of turnover could potentially be used (see Koleff *et al.*, 2003), the JI is appropriate for examining changes in similarities that result from alterations in the matching component of species in paired sites, and should be much less sensitive to changes in the non-shared components (see Fig. 1). EstimateS Win 7.51 (Colwell, 2005) was used to obtain the total number of species, number of shared species and the JI for each pairwise comparison.

Table 1. Introduction data for extraregional ungulates in South Africa (at the quarter-degree grid-cell (QDGC) resolution with earliest date of reported introduction) showing the correspondence between introduction data from the literature and *Landbou Weekblad* advertisement data for those places with ungulate introductions reported in the literature (Bigalke, & Bateman, 1962; Chapman & Chapman, 1980; Lloyd & Millar, 1983; Siegfried, 1962; Smithers, 1983; van Ee, 1962). Corresponding data are highlighted in grey.

QDGC	Introduction data from the literature.						Advertisement data from <i>Landbou Weekblad</i> (since 1965)					
	<i>Dama dama</i>	<i>Cervus elaphus</i>	<i>Kobus leche</i>	<i>Sus scrofa</i>	<i>Bubalus bubalis</i>	<i>Lama glama</i>	<i>Dama dama</i>	<i>Kobus leche</i>	<i>Bubalus bubalis</i>	<i>Sus scrofa</i>	<i>Lama glama</i>	<i>Cervus elaphus</i>
3226CB			1960s									
3226DC	1970s		1970s				1969					
3226CA	1970s		1970s				1982	1990				2004
3420CA	1970s	1970s										
3023CB	1970s											
2330CD	1970s						1984		1993			
3419AB	1970s	1970s		1970s								
3119BD	1970s						1990					
3318DC	1869			1970s			1973			1997		
3227AC	1970s						1997	2004				
3025CA	1970s											
3225BA	1970s						1991	2004				
2923BB	1970s								1967			
3327CC	1970s											
3326BC	1970s		1970s				1973					
3124AB	1970s											
3418BB	1938											
2924CA	1970s											
3126BB	1970s											
2921AC	1970s								1967			
2824DA	1970s		1970s		1970s	1970s	1996	1979	1996		1979	
3320BB	1970s						1980					
2525DC	1970s				1970s							
3126BD	1908						1989					
3126AD	1970s						1993					
3319CC	1970s			1970s			1968		1974			
3024AD	1970s											
3218DD	1970s	1970s										
2823AC	1970s											
3126DD	1970s											
3225DA	1970s						1990	2000				
3126DA	1970s						1976					
3125BD	1970s						2003					
3220BC	1970s											
3420AB		1970s										
3226AB	1970s						1990					

Table 1. continued.

2729BD	1900						1966	1973	1978			
2624DC	1970s						1976		1981	1976		
3319CB	1970s						1980					
2628DB	1978	1975					1977		1989			
2827DC		1895					2005					
2727BD	1972						1979					
2829AC	1900s						1967	1976	1976			
2827DD	1910						1976					
2926AA	1960s						1973	2003				
2627BD	1973						1978	1996		1998		

Because the pairwise values are not independent each other due to the same place being used in multiple comparisons, sensitivity analyses were used to determine the minimum number of data points that result in statistical significance for each analysis.

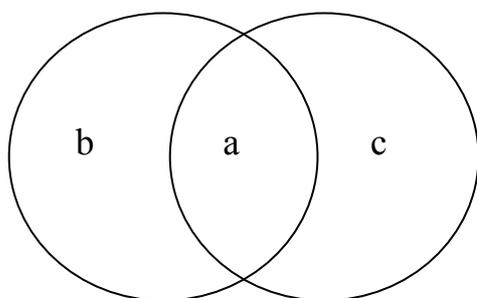


Figure 1. Schematic of the distribution of species across a pair of study sites. a) comprises the species that are shared by both sites, b) comprises the species that are unique to site one and c) comprises the species that are unique to site two. Figure adapted from Koleff *et al.* (2003).

Distance, spatial scale and species richness

A species-by-country matrix of indigenous ungulates was compiled to represent the state of the ungulate biota in countries globally before introductions and extirpations. Further matrices were compiled to represent the state of ungulate biotas after the introduction of non-indigenous species (recalling that only established introductions were considered), after extirpations (with and without the inclusion of IUCN red listed species as extirpated), and the combination of these processes. Fifty-one ungulates were recorded as endangered (or of higher threat category) by the IUCN (2006) and of these species thirty-two occur in, and would be lost from, the forty-one countries analysed. Only countries with both indigenous ungulates and established non-indigenous ungulates were included in the analyses. The mean country size for the

forty-one countries used in the analyses was 670 205 km² (data from ArcGIS 3.3, ESRI, 2002). Distance between the centroids of countries was calculated using Shirokov's spherical law of cosines (Dale, 2005).

At each spatial scale in South Africa species matrices were also constructed for indigenous ungulates and established introductions. At the QDGC scale matrices were compiled for extralimital and extraregional introductions. Only QDGCs with introduction data were included in analyses. Distance between degree grid-cells was calculated as above.

The importance of scale for analyses of homogenization was investigated in two ways. First, predicted mean homogenization was calculated using Generalized Linear Models (GLZs) (normal distribution, identity-link function) and compared for countries globally and at the QDGC, ODGC and TDGC scales in South Africa using the Wald chi-square test. Second, the relationship between homogenization and log₁₀ distance was assessed at each scale using a GLZ (normal distribution, identity-link function). Although the comparisons within South Africa concern a change in resolution whilst holding extent constant, the global scale analysis not only includes a change in extent, but also in resolution. The extent of the non-independence effect of the paired sites was examined by calculating the minimum number of data points that result in statistical significance. The estimates for the homogenization-distance relationships obtained from the models were then compared using the GT2 method (Sokal & Rohlf, 1997; p500), which is used to compare regression coefficients. Because Koleff *et al.* (2003) suggested that increasing scale leads to an increase in the number of shared species, and Olden (2006) proposed that homogenization increases with increasing scale and increased change in species richness, the relationships between homogenization and percentage change in species richness and between mean homogenization and the number of shared species were explored across spatial scales. Predicted mean homogenization, mean percentage change in species richness and mean shared species were obtained from GLZs (normal distribution, identity-link function), at the four different scales. Pearson's product moment correlations were then used to establish the relationships between mean homogenization and mean percentage change in species richness and between mean homogenization and the mean number of shared species at the three scales in South Africa.

To assess the contribution of species richness change to homogenization at the within-scale level, percentage change in species richness was calculated for each pairwise country comparison and for QDGCs in South Africa, as the total number of established non-indigenous ungulates at both sites divided by the total number of indigenous ungulates at both sites. The importance of species richness change for homogenization was then assessed in two ways. First, the relationship between homogenization and \log_{10} of the total number of non-indigenous ungulates was determined using GLZs (normal distribution, identity-link function) for countries globally and for QDGCs in South Africa. Second, to establish the relationship between homogenization and \log_{10} percentage change in species richness, as is more typically done (Olden 2006), GLZs (normal distribution, identity-link function) were used for countries globally and for QDGCs in South Africa. A log transformation was chosen over an ArcSin transformation as it was more appropriate for the data. Again, the extent of the non-independence effect was examined by calculating the minimum number of data points that result in statistical significance.

Extinctions, extraregional introductions, extralimital introductions and time

Two types of extirpations were considered on a country-by-country basis: those species that have been extirpated from countries globally (EXT) and endangered species that are likely to go extinct in the future (inclusive of those species already extirpated) (END). The importance of introductions versus extinctions in homogenization was established by comparing outcomes of homogenization due to five different scenarios: established non-indigenous species only (EST), extirpations only (both EXT and END), and a combination of established non-indigenous species and extirpations (both EST+EXT and EST+END). First, predicted mean homogenization as a consequence of EST, EXT, END, EST+EXT and EST+END was calculated using GLZs (normal distribution, identity-link function) and compared using the Wald chi-square test. Second, the relationships between homogenization as a result of EST, EXT, END, EST+EXT and EST+END and \log_{10} distance were assessed using GLZs (normal distribution, identity-link function). The extent of the non-independence effect was examined as above. The estimates for the homogenization–distance relationships for EST, EXT, END, EST+EXT and EST+END were then compared using the GT2 method (Sokal & Rohlf, 1997).

The relative contribution of extralimital versus extraregional introductions to homogenization at the QDGC scale in South Africa was determined in two ways. First, predicted mean homogenization as a result of extralimital introductions, extraregional introductions and all introductions was calculated using GLZs (normal distribution, identity-link function) and compared using Wald chi-square tests. Second, the relationships between homogenization as a result of extralimital introductions, extraregional introductions and all introductions and \log_{10} distance were assessed using GLZs (normal distribution, identity-link function). The extent of the non-independence effect was examined as above. The estimates for the homogenization–distance relationships were then compared using the GT2 method (Sokal & Rohlf, 1997).

Temporal trends in homogenization were investigated in South Africa at the QDGC scale for extraregional and extralimital introductions separately. Introduction data for more than 30 QDGCs were obtained between 1965 and 1971. For each year, from 1971 to 2005, mean homogenization resulting from extraregional introductions only and mean homogenization resulting from extralimital introductions only was calculated. For homogenization resulting from extraregional introductions, only QDGCs with extraregional advertisements were used in analyses. The same was done for extralimital advertisements. This approach results in a different calculation of homogenization to that above, where the contribution of homogenization due to extraregional and extralimital introductions was assessed for QDGCs with any introductions (extraregional or extralimital). The relationship between mean homogenization for each year and time was determined for extralimital and extraregional introductions using GLZs (normal distribution, identity-link function). Best subset models were built using time as both a linear and quadratic term, to determine whether a linear or quadratic function best fits the data. The Akaike Information Criterion was used to select the best model, with Akaike weight used to indicate the likelihood of a model being the best of the full set of models (Johnson & Omland, 2004).

Pathways and correlates of ungulate introductions

Initial assessments of data from Long (2003) and Lever (1985) suggested that ungulate introductions might be a consequence of the release of non-indigenous species from zoos. To determine whether zoos could be contributing to ungulate introductions globally, established non-indigenous ungulate data from Long (2003) and Lever (1985), and zoo holdings and transfer data from the International Species Information System (ISIS) database (ISIS, 2007) were used. Spatial autocorrelation in the data was investigated using correlograms constructed in SAM (Rangel *et al.*, 2006). Correlograms were constructed for each variable used in this analysis and the significance of each correlogram was determined by Oden's (1984) method. No significant spatial autocorrelation at $p < 0.05$ was found for any of the variables used in this analysis. Nonetheless, latitude and longitude were included in analyses. The relationships between the number of established non-indigenous ungulates and indigenous ungulate species richness, human population size, area of country, number of zoos in the country, number of indigenous ungulate species in zoos, non-indigenous ungulate species richness in zoos and the number of non-indigenous ungulate species sold from zoos to the public were assessed using GLZs (Poisson distribution, log-link function, corrected for overdispersion). Many of the predictor variables are highly correlated with each other (Table 2). Before best subset models were built, collinearity was examined and removed by selecting a subset of variables that had high tolerances (see Quinn & Keough, 2003: 128). The variables used for final model building included the number of ungulate species in zoos, indigenous ungulate species richness of the country in question, its area and the latitude and longitude of its central point. The Akaike Information Criterion was used to select the best model as above.

Table 2. Correlation matrix for the parameters used in Generalized Linear Model analyses for determining the best predictors of the number of established non-indigenous ungulates in each country. Significant correlations at $p < 0.05$ are in bold.

	EST	NI ZOO TO PUBLIC	ALL ZOO TO PUBLIC	NI ZOO	ALL ZOO	POP	AREA	LAT	LONG	INDIG	INDIG ZOO
EST	1.00	0.51	0.49	0.40	0.39	0.39	0.34	-0.31	0.16	-0.09	0.05
NI ZOO TO PUBLIC	0.51	1.00	1.00	0.78	0.82	0.58	0.24	0.20	-0.22	0.07	0.33
ALL ZOO TO PUBLIC	0.49	1.00	1.00	0.77	0.81	0.57	0.25	0.19	-0.23	0.12	0.38
NI ZOO	0.40	0.78	0.77	1.00	0.98	0.46	0.13	0.47	-0.07	-0.20	0.08
ALL ZOO	0.39	0.82	0.81	0.98	1.00	0.51	0.19	0.42	-0.07	-0.05	0.25
POP	0.39	0.58	0.57	0.46	0.51	1.00	0.66	0.08	-0.28	0.24	0.32
AREA	0.34	0.24	0.25	0.13	0.19	0.66	1.00	0.00	-0.03	0.30	0.35
LAT	-0.31	0.20	0.19	0.47	0.42	0.08	0.00	1.00	-0.12	-0.42	-0.21
LONG	0.16	-0.22	-0.23	-0.07	-0.07	-0.28	-0.03	-0.12	1.00	-0.07	-0.05
INDIG	-0.09	0.07	0.12	-0.20	-0.05	0.24	0.30	-0.42	-0.07	1.00	0.80
INDIG ZOO	0.05	0.33	0.38	0.08	0.25	0.32	0.35	-0.21	-0.05	0.80	1.00

EST: established non-indigenous ungulate introductions, NI ZOO TO PUBLIC: non-indigenous ungulate species sold from zoos to the public, ALL ZOO TO PUBLIC: all ungulate species sold from zoos to the public, NI ZOO: non-indigenous ungulate species in zoos in country, ALL ZOO: all ungulate species in zoos in country, POP: human population of country, AREA: area of country, LAT: latitude of country, LONG: longitude of country, INDIG: indigenous ungulate species richness of country and INDIG ZOO: number of indigenous ungulate species in zoos in country.

The relationships between the number of extralimital and extraregional introductions at the QDGC scale and indigenous ungulate species richness, livestock numbers, average annual income and human population density were assessed using GLZs (Poisson distribution, log-link function, corrected for over-dispersion where necessary). To investigate whether spatial autocorrelation is present in the introduction data or any of the predictor variables, correlograms were constructed using SAM as described above. The only variable that showed significant, but typically low values of spatial autocorrelation at $p < 0.05$, was indigenous ungulate species richness. Autocorrelation was therefore not given further consideration. In these analyses, tolerance was typically high for the independent predictors in the models and none were excluded. The Akaike Information Criterion was used to select the best model as above. Predictor variables were \log_{10} transformed before analyses.

Because the relationship between the number of extralimital introductions and indigenous ungulate species richness is confounded by the total possible number of extralimital introductions being dependent on the indigenous ungulate species richness of a QDGC a null model was run to determine whether there is a stronger relationship between extralimital introductions and indigenous ungulate species richness than would be expected. The null model was written in R (R Development Core Team, 2004). Randomised data sets were created for the QDGCs that reported extralimital advertisements during the period 1965 and 2005 (1 109 extralimitals in 264 QDGCs) by randomly assigning species to QDGCs using probabilities based on indigenous ungulate species richness of the QDGCs. Slopes and intercepts of the generalized linear model (Poisson distribution, log-link function) between extralimital advertisements and indigenous ungulate species richness were calculated for 10 000 iterations of the model. The observed slope and intercept were compared to that of the simulated data and p values were calculated by counting the number of values larger or smaller than the observed values.

Temporal trends in extraregional introductions were investigated by examining the relationship between the number of extraregional advertisements from 1965 until the relevant year and each predictor variable for each year, from 1971 to 2005, using GLZs (Poisson distribution, log-link function, corrected for over-dispersion where necessary). The relationships between time and the slopes (estimates) of the

relationships between the number of introductions and predictor variables for each year were determined for each predictor variable using GLZs (normal distribution, identity-link function). Best subset models were built using time as both a linear and quadratic term, to determine whether a linear or quadratic function best fits the data. The Akaike Information Criterion was used to select the best model, with Akaike weight used to indicate the likelihood of a model being the best of the full set of models (Johnson & Omland, 2004).

At the provincial scale in South Africa, the extent to which the number of non-indigenous ungulate introductions per province can be attributed to the hunting industry was investigated using data on the number of hunts, clients and game farms per province in South Africa obtained from Patterson & Khosa (2005). At the provincial scale, statistics for professional hunting and game farming in South Africa (Patterson & Khosa, 2005) were used to examine the role of the hunting industry in extraregional introductions. The relationships between the number of extraregional introductions per province and the number of game farms, clients and hunts for the 2003/2004 hunting season in South Africa as well as the predictor variables used at the QDGC scale were investigated using GLZs (Poisson distribution, log-link function, corrected for over-dispersion). Before best subset models were built collinearity between predictor variables was examined and removed as above. The variables used for final model building included the number of hunts per year, mean indigenous species richness, mean human population density, mean income and mean density of livestock. The Akaike Information Criterion was used to select the best model as above. Predictor variables were \log_{10} transformed before analyses.

RESULTS

Distance, spatial scale, and species richness

Ungulate faunas showed substantial homogenization at the local scale in South Africa (across 297 QDGCs, 91 ODGCs and 28 TDGCs), and globally for the 41 countries analysed (Figs 2 & 3). Many ungulate assemblages in close proximity to each other have become differentiated through introductions as they share more indigenous than introduced species. Over longer distances more introduced species than indigenous species are shared (Fig. 2, Table 3a).

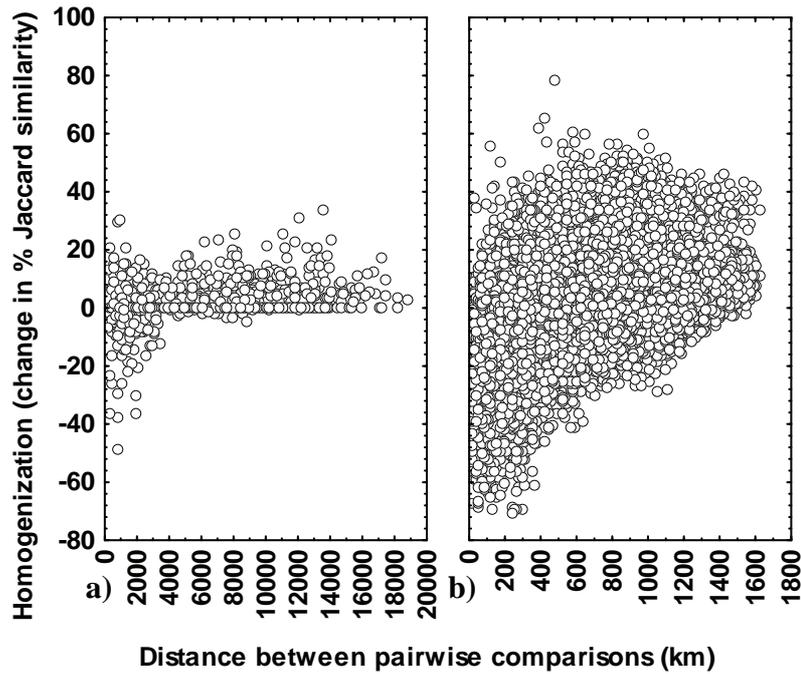


Figure 2. The relationship between homogenization and distance for a) countries globally (n = 820 pairwise comparisons) and b) quarter-degree grid-cells in South Africa (n = 73920 pairwise comparisons).

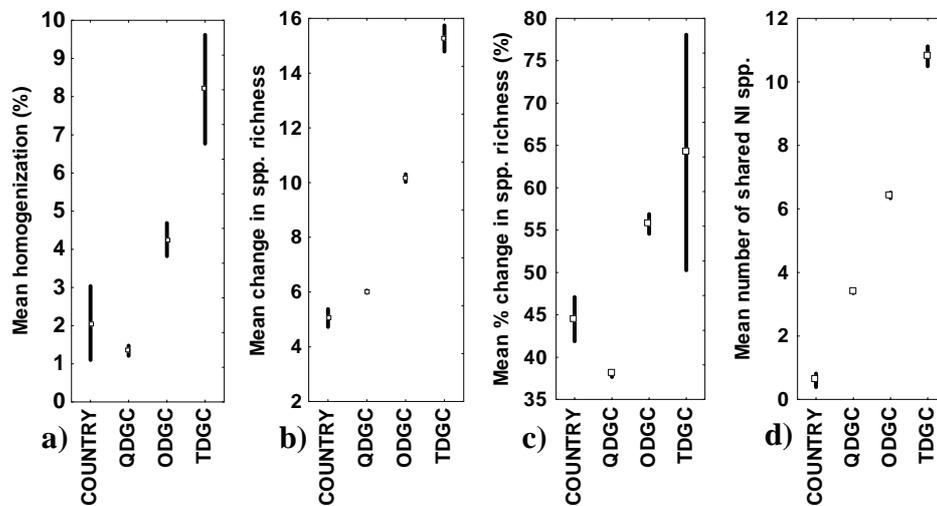


Figure 3. Predicted a) mean homogenization, b) mean change in species richness, c) mean % change in species richness and d) mean number of shared non-indigenous (NI) species with 95% confidence limits calculated using generalized linear models (normal distribution, identity-link function) for countries globally (n = 820 pairwise comparisons) and at the quarter-degree grid-cell (QDGC) (n = 73920 pairwise comparisons), one-degree grid-cell (ODGC) (n = 6786 pairwise comparisons) and two-degree grid-cell (TDGC) (n = 378 pairwise comparisons) resolution in South Africa.

Table 3. The contribution of a) scale (quarter-degree grid-cell (QDGC), one-degree grid-cell (ODGC) and two-degree grid-cell (TDGC)), b) introductions (EST) and extinctions (END and EXT) for 41 countries and c) extralimital (EXTRALIM), extraregional (EXTRAREG) and all (NI) introductions in South Africa at the QDGC resolution, to the relationship between homogenization and \log_{10} distance calculated using Generalized Linear Models (GLZs) (normal distribution, identity-link function).

a)	Estimate \pm standard error	Wald statistic	Min % data for $p < 0.05$	n
QDGC	21.4 \pm 0.2 ^A	11158	23	73920
ODGC	26.8 \pm 0.7 ^B	1470	33	6786
TDGC	29.4 \pm 2.5 ^B	134	37	378
Country	5.77 \pm 0.7 ^C	80	12	820
b)	Estimate \pm standard error	Wald stat	Min % data for $p < 0.05$	n
EST	5.77 \pm 0.7 ^A	80	12	820
EXT	-1.22 \pm 0.3 ^B	22	4	820
END	-4.99 \pm 0.4 ^C	157	21	820
EXT + EST	5.24 \pm 0.7 ^{AD}	59	9	820
END + EST	3.95 \pm 0.7 ^D	30	5	820
c)	Estimate \pm standard error	Wald stat	Min % data for $p < 0.05$	n
NI	21.4 \pm 0.20 ^A	11158	23	73920
EXTRAREG	6.74 \pm 0.08 ^B	8172	18	73920
EXTRALIM	18.2 \pm 0.20 ^C	7930	17	73920

Different superscript letters indicate significant differences between estimates from the GLZs based on the GT2 method. All Wald statistics are significant at $p < 0.001$. Min % data for $P < 0.05$, to account for non-independence in the data the minimum percentage of data that result in statistical significance at $p < 0.05$ is reported. n is the number of pairwise comparisons.

Within South Africa, mean homogenization increased significantly from the QDGC to TDGC scale (Fig. 3), with mean homogenization being significantly different at each scale ($X^2 = 238$, $p < 0.001$). However the relationship between homogenization and distance did not differ between the ODGC and TDGC scales (Table 3a). Significant relationships were found between mean homogenization and mean species richness ($r = 0.99$, $p < 0.001$) and mean homogenization and mean number of shared species ($r = 0.99$, $p = 0.01$) at the three local resolutions, but not between mean homogenization and mean percentage change in species richness ($r = 0.96$, $p = 0.184$).

At the QDGC scale within South Africa, increasing numbers of introductions typically resulted in differentiation of the ungulate fauna and this was true also of an increase in the percentage change in species richness (Table 4, Fig. 4). By contrast, at the global scale, homogenization increased with the number of established introductions, but no significant relationship was found between homogenization and percentage change in species richness (Table 4, Fig. 4). The primary reason for these differences between scales appears to be a stronger relationship between the number of introductions and percentage species richness change at the QDGC scale in South Africa ($r = 0.91$, $p < 0.001$) than between countries globally ($r = 0.53$, $p < 0.001$).

Extinctions, extraregional introductions, extralimital introductions and time

At the global scale, introductions (mean homogenization (H) = 2.07 ± 0.22 %) have resulted in significantly larger values of homogenization than realized extinctions (H = 0.44 ± 0.20 %; $\chi^2 = 34.20$, $p < 0.001$) and extinctions that have taken place do not significantly increase the level of homogenization above that due to introductions only (EXT+EST H = 2.32 ± 0.27 %; $\chi^2 = 0.49$, $p = 0.50$). When endangered taxa are presumed to become extinct, and when this value is added to known extinctions (END H = 1.34 ± 0.22 %), homogenization is significantly higher than that from realised extinctions ($\chi^2 = 21.32$, $p < 0.001$) but still lower than homogenization resulting from introductions ($\chi^2 = 5.5913$, $p = 0.018$). However homogenization as a result of introductions and additional extinctions (END+EST H = 2.83 ± 0.27 %) is significantly higher than homogenization due to current introductions by themselves ($\chi^2 = 4.00$, $p = 0.046$). By contrast, extinctions tend to reduce the slope of the positive relationship between distance and homogenization, because extinctions tend to differentiate more distant sites and homogenize sites in close proximity (Table 3b).

Table 4. The relationships between homogenization and non-indigenous species and homogenization and percentage change in species richness for 41 countries globally and at the quarter-degree grid-cell resolution (QDGC) in South Africa (SA) calculated using generalized linear models (GLZs) (normal distribution, identity-link function).

	Estimate ± s.e.	Wald statistic	Min % data for p < 0.05	n
log ₁₀ number of established NI species (Country)	6.24 ± 1.04	36	6	820
log ₁₀ number of established NI species (QDGC, SA)	-17.4 ± 0.24	5433	12	73920
log ₁₀ % change in species richness (Country)	-2.04 ± 1.04	4	n.s.	820
log ₁₀ % change in species richness (QDGC, SA)	-15.9 ± 0.15	11165	23	73920

Estimate ± s.e., estimate ± standard error of the GLZ relationship between homogenization and each parameter. Wald statistics are significant at p < 0.001. Min % data for P < 0.05, to account for non-independence in the data the minimum percentage of data that result in statistical significance at p < 0.05 is reported. n is the number of pairwise comparisons. n.s. indicates that the relationship is not significant.

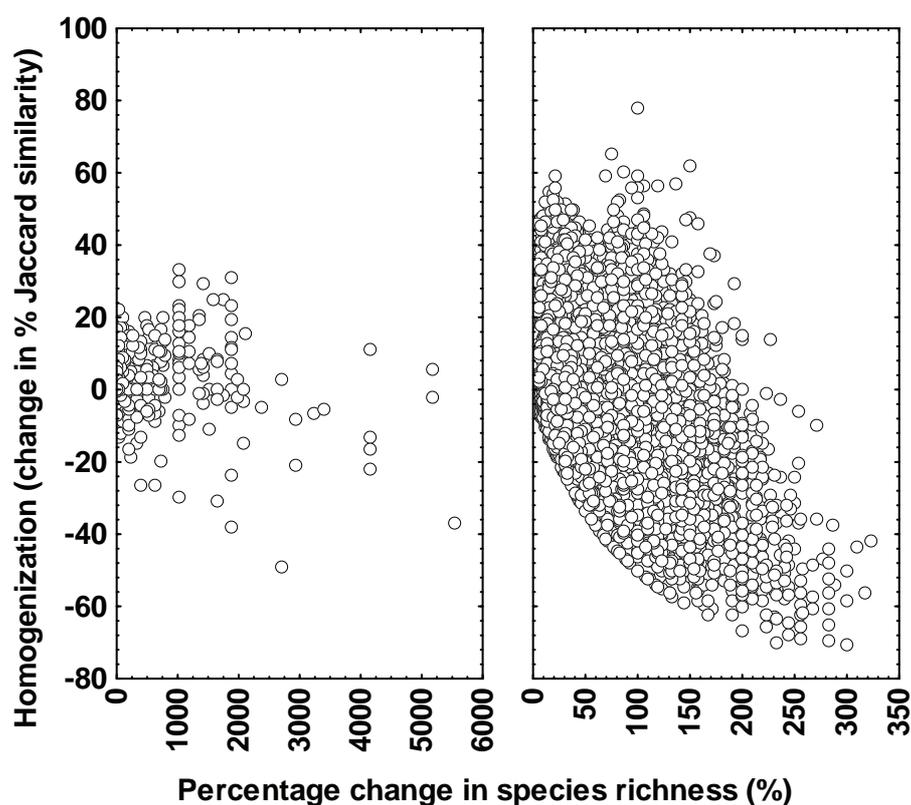


Figure 4. The relationship between homogenization and percentage change in species richness for a) countries globally (n = 820 pairwise comparisons) and b) quarter-degree grid-cells in South Africa (n = 73920 pairwise comparisons).

Extraregional and extralimital introductions make quite different contributions to homogenization in South Africa at the QDGC scale. Homogenization was most profoundly influenced by introductions of extralimital species ($H = 4.61 \pm 0.07 \%$) and extraregional ungulates tended to differentiate ungulate assemblages ($H = -3.83 \pm 0.07 \%$). The absolute extent of homogenization due to extralimital species was significantly higher than that due to extraregional introductions ($\chi^2 = 119.11$, $p < 0.001$) and extraregional introductions greatly reduced total homogenization when homogenization due to extralimital introductions was compared to homogenization resulting from all introductions ($H = 1.34 \pm 0.07 \%$; $\chi^2 = 1178.1$, $p < 0.001$). Likewise, a weaker relationship between distance and homogenization was found for extraregional than for extralimital introductions (Table 3c).

From 1965 to 2005, 18 species from outside South Africa were advertised in *Landbou Weekblad* magazine. Homogenization by extralimital introductions increased rapidly with time after initially having a smaller homogenizing effect than the differentiating effect of extraregional introductions (Fig. 5).

Pathways and correlates of ungulate introductions

Of the 47 countries for which data were obtained from the ISIS database, 32 countries had zoos that sold non-indigenous ungulates to private individuals during the period 1970 - 2005. 112 ungulate species were sold from zoos in countries to which they are not indigenous. Zoos in the United States sold 92 non-indigenous ungulate species, zoos in Germany 57, and zoos in South Africa, 32 non-indigenous ungulate species. Based on this information it seemed likely that zoos have provided a pathway of introduction for ungulate species in the past. The best fitting model for established, non-indigenous ungulate species in a country included the number of non-indigenous ungulate species in zoos in the country (strongly collinear with the number of non-indigenous ungulate species sold from zoos, see Table 2) indigenous ungulate species richness of the country, country area and longitude (Table 5a, Akaike weight $w_i = 0.60$). Established, non-indigenous ungulate species richness is high where indigenous ungulate species richness is low and many non-indigenous ungulate species are present in zoos.

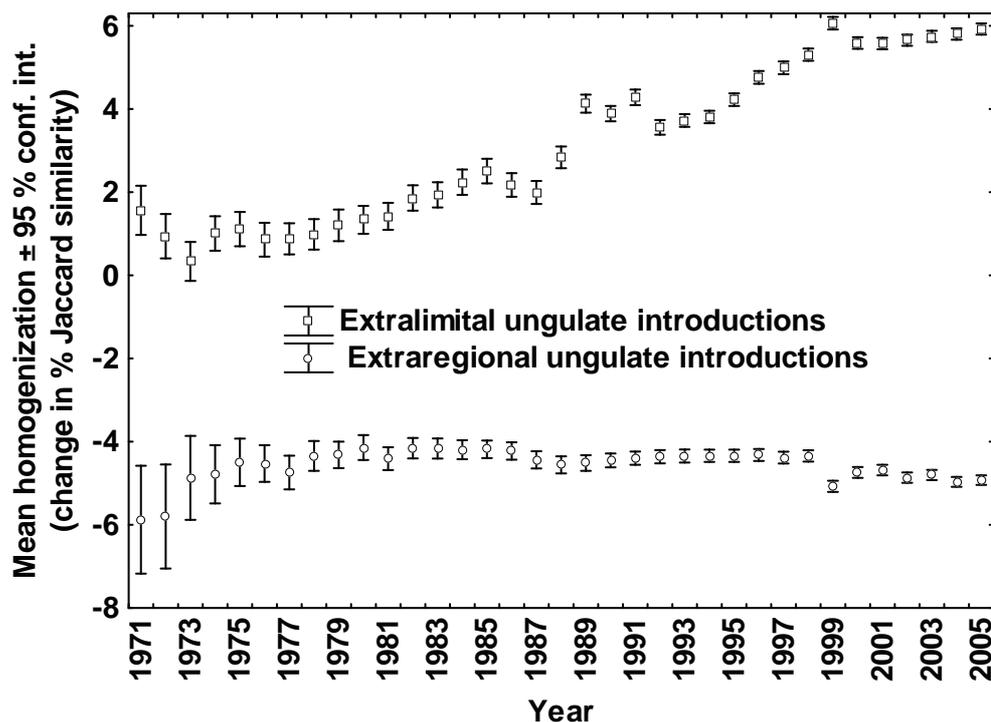


Figure 5. Temporal trends in homogenization as a result of extraregional (from 1971 (n = 190) to 2005 (n = 12246 pairwise comparisons)) and extralimital (from 1971 (n = 1035) to 2005 (n = 40186)) introductions in South Africa, at the quarter-degree grid-cell resolution, between 1971 and 2005. For extralimital introductions the equation for the relationship between homogenization and time is: $y = 0.0019x^2 + 0.11x + 0.39$ ($\chi^2 = 101$, $p < 0.001$), and for extralimital introductions the equation is: $y = -0.0035x^2 + 0.13x - 5.42$ ($\chi^2 = 36$, $p < 0.001$), where time = year – 1970. Both models had the highest Akaike weights ($w_i > 0.95$) relative to the other models examined.

Within South Africa, the best fitting model ($w_i = 0.70$) for numbers of extralimital introductions included all of the variables with the exception of income (Table 5b). The model indicates that numbers of extraliminally introduced species tend to be greatest in areas of low indigenous species richness, high human population density, and high livestock numbers. The null model for the relationship between extralimital introductions and indigenous ungulate species richness, controlling for the size of the extralimital species pool available for introduction, showed a significantly stronger slope ($p = 0.03$) and significantly larger intercept ($p < 0.001$) than that of the observed data. This indicates that relatively more extralimital species are being introduced to species rich areas than would be expected.

Table 5. The top three Generalized Linear Models (Poisson distribution, log-link function, corrected for overdispersion) for a) the number of established non-indigenous ungulates in each country, b) the number of extralimital ungulates per quarter-degree grid-cell (QDGC) in South Africa (SA) and c) the number of extraregional ungulates per quarter-degree grid-cell in South Africa.

a) Number of established non-indigenous ungulates in each country	AIC	w_i	χ^2	n
$\text{NISPPZOO}^{0.02} + \text{INDIG}^{-0.03} + \text{AREA}^{0.00} + \text{LAT}^{-0.02}$	123	0.60	61	41
$\text{NISPPZOO}^{0.02} + \text{INDIG}^{-0.03} + \text{AREA}^{0.00} + \text{LAT}^{-0.02} + \text{LONG}^{\text{NS}}$	125	0.22	61	41
$\text{NISPPZOO}^{0.02} + \text{INDIG}^{-0.03} + \text{LAT}^{-0.02}$	126	0.13	53	41
b) Number of extralimital ungulates per QDGC in SA	AIC	w_i	χ^2	n
$\text{INDIG}^{-0.04} + \text{POP}^{0.28} + \text{LIVESTOCK}^{0.40}$	753	0.70	77	284
$\text{INDIG}^{-0.04} + \text{POP}^{0.28} + \text{LIVESTOCK}^{0.40} + \text{INCOME}^{\text{NS}}$	754	0.30	77	284
$\text{POP}^{0.28} + \text{LIVESTOCK}^{0.40}$	776	0.00	51	284
c) Number of extraregional ungulates per QDGC in SA	AIC	w_i	χ^2	n
$\text{POP}^{0.26} + \text{INCOME}^{1.14} + \text{LIVESTOCK}^{0.23}$	483	0.45	20	157
$\text{POP}^{0.26} + \text{INCOME}^{1.14} + \text{LIVESTOCK}^{0.23} + \text{INDIG}^{\text{NS}}$	485	0.16	20	157
$\text{POP}^{0.26} + \text{LIVESTOCK}^{1.14}$	486	0.14	15	157

Best subset models were selected using Akaike Information Criterion (AIC) and Akaike weights (w_i). The estimate of the relationship is in superscript for each predictor variable. NS indicates that the relationship is not significant. All maximum log likelihood ratio Chi-square (χ^2) results were significant at $p < 0.001$. n is the number of pairwise comparisons.

NISPPZOO: number of non-indigenous ungulate species in zoos, INDIG: indigenous ungulate species richness, AREA: area of country, LAT: latitude of country, LONG: longitude of country, POP: human population density, LIVESTOCK: total livestock numbers, INCOME: mean annual income.

For extraregional introductions the best fitting model ($w_i = 0.45$) suggested that the numbers of extraregionally introduced species tended to be largest in areas with greatest population density, largest numbers of livestock, and where income was largest (Table 5c), but in the past extraregional ungulate species were introduced to areas species poor for ungulates and areas less productive for livestock (Fig. 6).

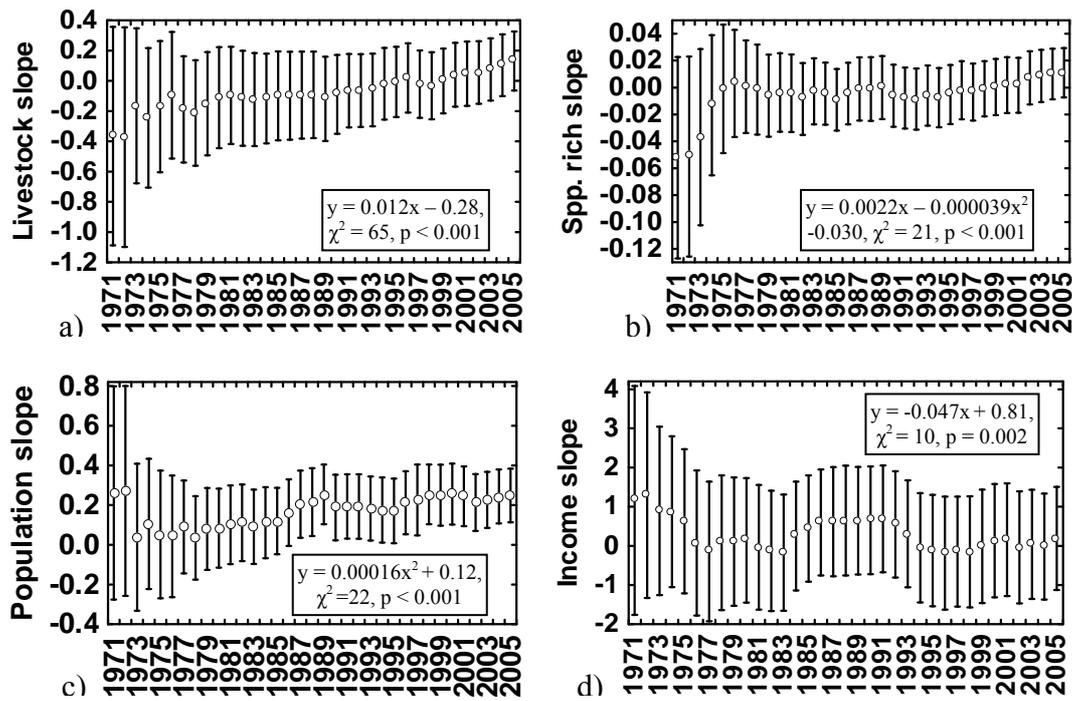


Figure 6. Plots of the estimates (slopes) with 95 % confidence limits of the relationships between the number of extraregional ungulate advertisements per QDGC and a) livestock numbers, b) indigenous ungulate species richness, c) human population size and d) average annual income for years 1971 to 2005. For each year a negative value represents a negative relationship, and a positive value a positive relationship (Generalized Linear Model (GLZ) (Poisson distribution, log-link function)) between the number of extraregional ungulate advertisements from 1965 until that year and the predictor variable. Inserts represent the best GLZ (normal distribution, identity function) relationship when using time and time² as predictor variables, where time = year – 1970.

At a provincial level, the best fitting model ($w_i = 0.69$) for extraregional ungulate species in provinces in South Africa included the density of game farms, indigenous ungulate species richness, human population density and average annual income (Table 6).

Table 6. The top three Generalized Linear Models (Poisson distribution, log-link function, corrected for overdispersion) for the number of extraregional ungulates per province in South Africa. Best subset models were selected using Akaike Information Criterion (AIC) and Akaike weights (w_i). The direction of relationship is in superscript for each predictor variable. NS indicates that the relationship is not significant. All maximum log likelihood ratio Chi-square (χ^2) results were significant at $p < 0.001$.

	AIC	w_i	χ^2
GFARMS ⁺ + INDIG ^{NS} + POP ^{NS} + LIVESTOCK ^{NS}	145	0.69	1646
GFARMS ⁺ + INDIG ^{NS} + POP ^{NS} + LIVESTOCK ^{NS} + HUNTS ^{NS}	146	0.31	1646
GFARMS ⁺ + INDIG ^{NS} + LIVESTOCK ^{NS} + HUNTS ^{NS}	185	0.00	1605

GFARMS: density of game farms, INDIG: indigenous ungulate species richness, POP: human population density, LIVESTOCK: total livestock numbers, HUNTS: density of hunts.

DISCUSSION

Distance and spatial scale

In keeping with Olden & Poff's (2003) predictions, and other empirical work (Qian & Ricklefs, 2006, but see also McKinney, 2004a, b for contrasting findings), introduced species increased differentiation at small distances, but reduced it over large ones. This outcome was largely a result of positive autocorrelation of indigenous assemblages over shorter distances (Thomson *et al.*, 1996; Legendre & Legendre, 1998; van Rensburg *et al.*, 2002), which increases the likelihood that introduced species will differentiate assemblages in close proximity to each other. By contrast, more distant sites will be more different than expected by chance, and the addition of introduced species therefore has a greater likelihood of increasing their similarity. At the largest distances (c. > 10 000 km), globally, countries share no indigenous species. In consequence, differentiation cannot proceed further, resulting in a hard boundary at 0% change (Fig. 2). Above these distances, the only possibility of multiple introductions is either no change in homogenization, or an increase thereof. As

distance between sites declines below this threshold, which is likely to be taxon-specific given differences between groups in average range sizes and dispersal abilities (Brown *et al.*, 1996; Gaston, 2003; Lester *et al.*, 2007), an increasing number of species will be shared, enabling the differentiation of sites with the addition of new species.

Changes in the resolution and extent of studies are expected to influence values of homogenization (see Olden & Poff, 2003 and below). Nonetheless, with adequate recognition of the influence of scale on homogenization, the present results can be compared with those of previous studies conducted using Jaccard's index of similarity (Table 7). The largest extent analysed to date using species identities and JI has been plants in North America at the province and state resolution (Rejmánek, 2000; Qian & Ricklefs, 2006). The largest resolution examined has been territories and provinces in Canada (Taylor, 2004). Whilst narrower in extent than the present work, it is nonetheless clear that homogenization values found here at the global scale (2 %) are larger than those found for plants in North America (Rejmánek, 2000; Qian & Ricklefs, 2006) and fish in Canada (Taylor, 2004), but less than those found for fish in the United States (Rahel, 2000).

Like the QDGC scale data used in this study, the finest resolution studies that have been conducted are not contiguous (Radomski & Goeman, 1995; McKinney, 2004b; Castro *et al.*, 2007). The homogenization results for plants (McKinney, 2004a; Castro *et al.*, 2007) compare well with homogenization seen at the QDGC scale here (1 %). The TDGC resolution (8 % homogenization) can be compared with studies on fish at a zoogeographic province resolution in California (Marchetti *et al.*, 2001) and basin resolution in the Iberian peninsular (Clavero & García-Berthou, 2006), which in both cases show much higher homogenization than was documented here.

Table 7. Extent and resolution of homogenization studies conducted using Jaccard's index of similarity. Area of extent and resolution were estimated using area data from the internet and dividing the area of extent by the number of sites for contiguous studies. Table adapted from Olden (2006).

Taxon	Extent	Total area (km ²)	Resolution	Number of sites	Mean area of sites (km ²)	Mean Δ similarity (%)	Reference
fish	Minnesota	225181	lakes	62	90	9	Radomski & Goeman, 1995
fish	California	423999	watersheds	43	9860	-10.7	Marchetti <i>et al.</i> , 2001
fish	Iberian peninsular	582860	hydrographic units (basins)	10	58286	17.1	Clavero & Garcia-Berthou, 2006
fish	California	423999	zoogeographic provinces	6	70667	20.3	Marchetti <i>et al.</i> , 2001
fish	British Columbia	944735	aquatic ecoregions	8	118092	-3.5	Taylor, 2004
fish	United States	8103674	states	48	168827	7.2	Rahel, 2000
fish	Canada	9984670	territories / provinces	13	768052	1.3	Taylor, 2004
herptiles	Florida	170312	counties	12	2542	-0.01	Smith, 2006
plants	United States	8103674	parks and local areas	20	16	0.80	McKinney, 2004b
plants	island archipelagoes	351	islands	6	58	2.0	Castro <i>et al.</i> , 2007
plants	North America	18088344	states	60	296530	0.012	Qian & Ricklefs, 2006
plants	North America	18088344	states / provinces	30	296530	-0.6	Rejmánek, 2000

In keeping with Olden's (2006) prediction, homogenization increased with a decline in spatial resolution. Differential detectability or observation of introductions and extinctions (Olden & Poff, 2003; Olden, 2006) cannot account for this result given the way in which this study was done. Rather, the change in homogenization was likely a consequence solely of the way grain influences patterns of spatial autocorrelation among indigenous species and among introductions. Generally, it is expected that the matching (or shared species) component (see Fig. 1) of the JI will increase with coarser grain owing to growing positive autocorrelation, and therefore growing continuity among pairwise site comparisons (Lennon *et al.*, 2001). In consequence, the increase in homogenization with coarser grain size found here means that the numbers of introduced species common to assemblages in paired sites must increase more rapidly than the number of indigenous species common to both assemblages. Clearly, at some point this differential will not be sustainable, and therefore one might expect a decline as resolution becomes even coarser. This effect likely explains the similarity between the homogenization values at the global and QDGC scales found in the present study.

Whilst the JI is also sensitive to total species richness and to richness differences between sites (Lennon *et al.*, 2001; Koleff *et al.*, 2003), its behaviour provides a measure of homogenization, owing to the introduction of non-indigenous species, that accords with expectation. In other words, homogenization is recorded as greater when a fixed number of new shared species is added to species poor assemblages, than when the same number of shared new species is added to species rich assemblages. Likewise, if species richness differs between assemblages, the symmetry of the index means that it is relatively insensitive to these differences so long as they are largely restricted to the non-shared component (see Fig. 1) of the assemblages (see Koleff *et al.*, 2003). By contrast, differences in the matched component of assemblages mean substantial changes in the JI, which is precisely what is meant by homogenization via the introduction of new, shared species. Olden & Poff (2003) criticized change in the JI as a measure of homogenization when they noted that this measure results in an 'inflation' of homogenization in species poor assemblages by comparison with species rich assemblages. At least on a species richness basis (i.e. ignoring the fact that single species can have substantial impacts on whole systems – e.g. Courchamp *et al.*, 2003; O'Dowd *et al.*, 2003), it this 'inflation' is precisely what should be

recorded as homogenization. Two assemblages that previously had a total of ten species, of which five were shared, and which following introductions, have an additional five shared species are clearly more homogenized than two assemblages that have a total of 200 species, with 100 shared initially, and 105 shared following invasion. Although many other indices of turnover exist, they often show complex patterns of response of each of the components to changing richness. Moreover, in several cases they are more sensitive to species gains and losses than to continuity (reviewed in Koleff *et al.*, 2003). If the aim of a study is to document homogenization as a consequence of species extinctions (a significant component of the homogenization process – see McKinney & Lockwood, 1999), then some of these other indices may be more useful than the JI, especially because the JI is much less sensitive to losses of non-shared species than it is to gains of shared species. However, when homogenization as a consequence of introductions is the major focus of an investigation, then the JI is appropriate.

Species richness and homogenization

The influence of a change in species richness on homogenization differed between South Africa (at QDGC scale) and the global investigation. In the former case, both an increase in numbers of introduced ungulate species and an increase in the percentage species richness of a pair of sites resulted in differentiation of the assemblages. The similarity of these results is a consequence of the strong relationship between the number of introduced species and change in percentage species richness. Sites with the greatest change in percentage species richness (and highest number of introductions) tend to have been species poor sites where different new ungulate species were added. However, this tendency shows considerable variation, and it is clear from Fig. 4 that a site showing 100% increase in richness could either show homogenization or differentiation. Moreover, a lower bound to differentiation also exists as a consequence of different introductions to initially identical assemblages (Fig. 4). For example, if two assemblages with a Jaccard similarity of 1, i.e. $b = c = 0$ (see Fig. 1), face an increase in species richness of 50%, where none of the introduced species are shared, $\text{differentiation} = 1 - (a / (0.5 * a + a)) = 0.3333$. Where a , = number of shared species initially and, in this case, a also = total number of species initially. Maximal change in similarity is likely to be reached in instances where two assemblages originally have no species in common, and the

introduced species are those already indigenous to one of the assemblages (though they may come from elsewhere in their range). Olden (2006) showed a strong positive logarithmic relationship between homogenization and percentage change in species richness for fish and plants using previously published datasets. Marchetti *et al.* (2001) and Rooney *et al.* (2004) show positive linear relationships, in fish and plants, respectively. However, homogenization in South African ungulates shows a negative relationship with percentage change in species richness due to large numbers of different ungulate species introductions to species poor assemblages.

At the global scale, the relationship between the number of introduced species and percentage change in species richness is weak ($r = 0.53$, $p < 0.001$), so accounting for the significant relationship between homogenization and number of ungulate introductions, but the absence of such a relationship with percentage change in species richness. In other words, large numbers of additions do not typically lead to large changes in percentage species richness and *vice versa*. Overall, at the global scale the effect of changing species richness on homogenization was generally weak, and although it was positive, the data showed much variation.

Homogenization, extinctions, and the provenance of introductions

At the global scale, extinctions contributed only marginally to changes in homogenization (typically less than 0.5 %). However, when extinctions predicted on the basis of IUCN endangerment criteria (a pessimistic, but perhaps not entirely unrealistic outlook – Lawton & May, 1995; Ceballos & Ehrlich, 2002; Thomas *et al.*, 2004) were incorporated into the analyses, the resultant changes in homogenization significantly increased homogenization by introductions only. Indeed, homogenization by extinction may be an underestimate given that the JI is typically less sensitive to changes in species gains and losses than to changes in species continuity (Koleff *et al.*, 2003). However, using indices that are more sensitive to gains and losses invariably means underestimating changes in continuity, and therefore no additional analyses were undertaken here. Nonetheless, these results show that whilst introductions may presently be the major cause of homogenization due to larger numbers of introductions than extinctions (see also Gaston *et al.*, 2003), this situation could change as extinction proceeds and larger numbers of species go extinct (McKinney & Lockwood, 1999). Moreover, the spatial pattern of this

homogenization is likely to be complex given that extinctions (both realized and predicted) are likely to produce increasing differentiation with increasing distance between sites, whilst introductions often have the opposite effect.

Despite the recognition that the introduction of species to areas outside their typical range in a given country constitutes an introduction (McKinney, 2001, 2005; Copp *et al.*, 2005), such extralimital introductions are only beginning to be investigated from the perspective of taxonomic homogenization (McKinney, 2005). However, translocations of this nature have long been of conservation concern because of the likelihood of interspecific hybridization (Fabricius *et al.*, 1988), and because such introductions may have substantial influences on local ecosystems from which they were previously absent (e.g. Bond & Loffell, 2001). This work demonstrates not only that extralimital introductions are the major source of homogenization of ungulate assemblages in South Africa, and that they tend to increase the similarity of distant sites more substantially than extraregional introductions, but also that over time the increase in homogenization owes more to translocations within the country than to the introduction of species from outside the country. Whilst extraregional introductions can clearly lead to substantial impacts on systems (and the invasions literature is concerned largely with such impacts – Vitousek *et al.*, 1996; Chapin *et al.*, 2000; Mooney & Cleland, 2001; Courchamp *et al.*, 2003; Olden *et al.*, 2004; Clavero & García-Berthou, 2005), the potential for changes in patterns of diversity and system functioning as a consequence of translocations should not be underestimated.

Pathways and correlates of introduction

At present, the predictors of numbers of extralimital and extraregional introductions are similar. More species are introduced to areas with higher incomes and greater livestock density than the converse, probably reflecting the tendency of game farms and similar operations to introduce species from elsewhere (Table 6). One exception was the tendency for extralimital introductions to take place to areas with low indigenous species richness. The large available pool of extralimital species for introduction to species poor areas can account for the relationship, which also bears out the suggestion that introductions are made to increase diversity in areas that are ‘devoid’ of ungulate species to attract hunting or ecotourism clients (Castley *et al.*,

2001). The closest analogy is the introduction of game fish to areas with low indigenous fish diversity (McKinney, 2001).

In the past, introductions may have taken place for different reasons. When relationships between the numbers of extraregional introductions and each of the independent variables were examined year-by-year, initially the trends were quite different to those found presently (Fig. 6). That is, new extraregional ungulate species tended to be introduced to areas that were species poor for indigenous ungulate species and less productive for livestock (Fig. 6). However, the trend gradually vanished, with income and population density remaining as the major predictors (Fig. 6). In other words, through time, more introductions have been made to higher income, more densely populated areas than to others. The influence of large urban areas placing larger numbers of game advertisements cannot account for the trend because it remains when data from these areas are excluded from the analysis (results not shown).

In many ways, the present (rather than the presumed historical) correlates accord with what has been found in other studies. For example, McKinney (2001) found significant positive relationships between non-indigenous plant species richness and human population density in the United States as did Smith (2006) for herptiles in Florida and McKinney (2006a) for mammals, herptiles and plants at a global scale. These relationships between non-indigenous species and human population numbers are likely related to propagule pressure (Williamson, 1996; Colautti *et al.*, 2006), and to the circumstances that promote higher species richness generally.

In the latter case, indigenous and introduced species richness are strongly related at large spatial scales both in South Africa (Richardson *et al.*, 2005) and elsewhere (e.g. Chown *et al.*, 2005; Fridley *et al.*, 2007), as are indigenous species richness and human population density (Chown *et al.*, 2003; Gaston, 2004). Nonetheless, in other taxa, such as non-indigenous fish in the United States (McKinney, 2001) and birds globally (McKinney, 2006b), introduced species richness is not significantly related to human population density.

At the global scale, these analyses suggest that introductions tend to take place to species poor countries and, curiously, that introductions are positively related to the numbers of non-indigenous ungulate species in zoos in that country. Whilst the latter relationship does not necessarily imply cause and effect, it is clear from the ISIS database that zoos sell off their surplus animals to non-zoo recipients. The number of non-indigenous ungulate species sold from zoos in a country is also strongly correlated with the number of ungulate species in zoos in that country (Table 2). Sales from zoos are often the subject of a formal permitting process (at least in some provinces of South Africa), and will not necessarily lead to the kinds of consequences that invasive, as opposed to introduced, naturalized species (see Pyšek *et al.*, 2004 for definitions), will have for conservation. Nonetheless, that any relationship at all between numbers of established introductions and numbers of zoo holdings should exist is cause for at least some concern. Although the relationship may well be due to an unrelated, underlying variable, it does suggest that the manner in which zoos deal with surplus animals needs to be given some thought. Of course not all *ex-situ* conservation results in surplus stock contributing to the supplementation of indigenous populations.

In conclusion, this study of homogenization in ungulates in many ways bears out theoretical expectations and empirical findings from other groups. It indicates that homogenization in ungulates has taken place, and that extralimital introductions may be of considerable significance in the process regionally. The results indicate that increasing attention will have to be given to the conservation consequences of ungulate translocations, both within particular geopolitical regions and across the globe.

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- Chapter III -

Ungulate translocations as a conservation concern

In press:

Spear, D. & Chown, S.L. (in press). The extent and impacts of ungulate translocations: South Africa in a global context. *Biological Conservation*, doi:10.1016/j.biocon.2008.10.031

INTRODUCTION

Non-indigenous ungulate species are thought to pose a threat to biodiversity. They might hybridise with indigenous ungulates (Goodman *et al.*, 1999), compete with several taxa (Baccus *et al.*, 1985; Côté, 2005), host foreign pathogens and parasites (Meltzer, 1993; Cunningham, 1996), alter ecosystem functioning (Wardle *et al.*, 2001; Bayne *et al.*, 2004), and cause extinctions. Indeed, concerns about the effects of non-indigenous ungulates continue to grow (Cooke & Farrell, 2001; Roemer *et al.*, 2002; Husheer, 2007). By contrast, the ecological benefits of introductions are also widely recognized. These include re-introductions and restocking (Griffith *et al.*, 1989), enhancement of genetic diversity of inbred populations (Moritz, 1999; Storfer, 1999), and restoration of ecosystem function, including by the controversial process of ‘re-wilding’ (Donlan, 2005; Zimov, 2005). Likewise, substantial economic benefits from ungulate introductions have also been realized (e.g. from hunting Hofer, 2002; Loveridge *et al.*, 2006).

Despite the fact that ungulate introductions may have both substantial costs and substantial benefits, and the fact that ungulates can be counted among the most invasive species globally (Lowe *et al.*, 2000), the last two decades have seen little research quantifying introduction and translocation patterns and the extent to which the proposed negative impacts thereof have been realized. Indeed, over this period, only c. 50 readily accessible studies have been published in the Anglophone literature on the realized effects of ungulate introductions, most of which concern impacts on vegetation (see Box 1). Thus, little information is available regarding important aspects of introductions such as their pathways, frequency and number (i.e. propagule pressure) - which are important determinants of establishment success and invasion (Williamson, 1996; Lockwood *et al.*, 2005), and the extent to which plausible conservation concerns are being realized (though see Dolman and Wäber, 2008).

Box 1.

Methods

The last 20 years of literature demonstrating the impacts of non-indigenous ungulates on biodiversity was searched using ISI Web of Science (1988-2007). As ISI Web of Science limits the number of search terms used to 50 small sets of genera and vernacular names were used for searching together with the rest of the search terms. All searches made are represented by the following Boolean string:

(Addax or Aepyceros or Alcelaphus or Alces or Ammodorcas or Ammotragus or Antidorcas or Antilocapra or Antilope or Babyrousa or Bison or Beatragus or Blastocerus or Boselaphus or Bubalus or Budorcas or Camelus or Capreolus or Capricornis or Catagonus or Cephalophus or Ceratotherium or Cervus or Connochaetes or Dama or Damaliscus or Dicerorhinus or Diceros or Dorcatragus or Elaphodus or Elaphurus or Equus or Eudorcas or Eudorcus or Gazella or Giraffa or Hemitragus or Hexaprotodon or Hippocamelus or Hippopotamus or Hippotragus or Hydropotes or Hyemoschus or Hylochoerus or Kobus or Lama or Litocranius or Madoqua or Mazama or Moschiola or Moschus or Muntiacus or Naemorhedus or Nanger or Neotragus or Okapia or Odocoileus or Oreamnos or Oreotragus or Oryx or Ourebia or Ovibos or Ovis or Ozotoceros or Pantholops or Pecari or Pelea or Phacochoerus or Philantomba or Potamochoerus or Procapra or Przewalskium or Pseudois or Pseudoryx or Pudu or Rangifer or Raphicerus or Redunca or Rhinoceros or Rucervus or Rupicapra or Rusa or Saiga or Sus or Sylvicapra or Syncerus or Tapirus or Taurotragus or Tayassu or Tetracerus or Tragelaphus or Tragulus or Vicugna or ungulate or impala or hartebeest or elk or moose or dibatag or “Barbary sheep” or aoudad or springbok or pronghorn or blackbuck or deer or babirusa or bison or gaur or yak or banteng or kouprey or aurochs or nilgai or buffalo or anoa or tamarau or takin or camel or tur or markhor or roe or serow or peccary or duiker or rhino or wildebeest or topi or tsessebe or bontebok or blesbok or beira or ass or zebra or onager or kiang or gazelle or giraffe or tahr or hippo or Taruca or guemal or “roan antelope” or “sable antelope” or chevrotain or hog or waterbuck or kob or lechwe or puku or guanaco or gerenuk or dikdik or brocket or bororo or antelope or suni or “mountain goat” or klipspringer beisa or gemsbok or oribi or muskox or argali or mouflon or “Bighorn sheep” or “Dall's sheep” or “snow sheep” or chiru or rhebok or warthog or bushpig or bharal or siola or pudu or reindeer or steenbok or grysbok or reedbuck or Barasingha or chamois or saiga or “Palawan pig” or “bearded pig” or “Heude's pig” or “warty pig” or “wild boar” or tapir or eland or nyala or bongo or kudu or bushbuck or sitatunga or mouse-deer)
 AND (introduced or introduce or alien or extralimital or exotic or invasive)
 AND (impact or effect or damage or competition or compete or hybrid or vegetation or disease or pathogen or parasite)
 NOT (livestock or domestic or “invasive plant” or “alien plant” or “exotic plant”)

Results

Table 1. The number of papers demonstrating the impacts of non-indigenous ungulates on biodiversity.

<u>Demonstrated impacts of non-indigenous ungulates</u>	<u>Number of papers</u>
Vegetation alteration by herbivory	31
Indirect effects e.g. competition and hyper-predation	7
Habitat alteration by rooting e.g. soil erosion	7
Hybridisation	2
Parasite transmission	2
Predation	1

This general scarcity of information is true also for those countries, such as the United States (Butler *et al.*, 2005), Chile (Jaksic, 1998) and South Africa, that have substantial numbers of introduced ungulates and active translocation programmes.

Although South Africa has a rich indigenous ungulate fauna (Skinner and Chimimba, 2005), it also has a substantial history of ungulate introductions and translocations of indigenous ungulates to areas outside of their presumed historical ranges (extralimital introductions) (e.g. Lloyd & Millar, 1983; Brooke *et al.*, 1986). Both extralimital and extraregional ungulates are often introduced by landowners for financial reasons (Castley *et al.*, 2001; Lindsey *et al.*, 2006). Nonetheless, concerns have frequently been raised about the potential conservation implications of these actions (e.g. Brooke *et al.*, 1986; Bothma, 2005). Indeed, laws have recently been enacted under which the translocation and introduction of large mammal species are to be carefully regulated (National Environmental Management: Biodiversity Act: Anonymous, 2004). However, this Act has proven controversial among the game and hunting industries partially because they remain of the view that evidence for the negative impacts of non-indigenous ungulates in South Africa is limited (S.L.C. personal observations at Ministerial Stakeholder meeting, February 2007). For this reason, and because of relatively accessible information on introductions and translocations (e.g. Penzhorn, 1971), South Africa makes an excellent case study for quantifying the extent of ungulate translocations and introductions, investigating the pathways involved, and determining the extent to which proposed conservation problems associated with introductions have been realized.

Therefore, the aim of this study is to address these questions, which are of considerable significance more broadly, using the South African situation as an exemplar. To do so I adopt several approaches. First, to assess the extent of introductions in South Africa relative to the global situation, and the extent to which species introductions are influenced by indigenous species richness (the rich get richer hypothesis – see Stohlgren *et al.*, 1999), the relationship globally between numbers of indigenous and introduced ungulates is examined within countries. Next, temporal trends in ungulate introductions into the country are investigated to determine whether rates of introduction and translocation are increasing, whether zoos might serve as a pathway for introductions, and the distances over which ungulate translocations have

taken place. To determine the extent to which proposed impacts have been realized by these introductions I assess documented, rather than hypothesised, impacts of ungulate introductions in South Africa, and the extent of change in geographic range size that has been a consequence of translocations. The latter is especially significant given that much emphasis, both in South Africa (Erasmus *et al.*, 2002) and globally (Thomas *et al.*, 2004; Parmesan, 2006), has been placed on climate change-effected alterations of geographic range size. However, for widely traded species, range alterations through direct human actions may be as extensive as those that are predicted to be caused by climate change. Finally, given that a paucity of documented impacts does not necessarily mean that such impacts are not being realized, areas in South Africa which might be considered to be of potential conservation concern are also assessed owing to high introduction activity coupled with the presumed impacts of ungulate introductions.

METHODS

This study focuses on the orders Artiodactyla and Perissodactyla (following Wilson and Reeder, 2005). Although this is a polyphyletic grouping (e.g. Bininda-Emonds *et al.*, 2007) it is useful because the ungulates are typically considered distinct from other taxa, especially by the hunting industry, which is responsible for many translocations (Castley *et al.*, 2001; Long, 2003). Domestic goats, sheep, donkeys and cattle were excluded from analyses as these species are not species that are hunted for sport.

Ungulate introductions globally

To determine whether indigenous ungulate species-richness plays a role in the numbers of ungulate introductions, indigenous ungulate species-richness data were obtained for countries globally from Wilson and Reeder (2005), and for introduced ungulates from Siegfried (1962), Lloyd and Millar (1983), Lever (1985), Brooke *et al.* (1986), Mungall and Sheffield (1994), Castley *et al.* (2001), Forsyth and Duncan (2001), Hofer (2002), Long (2003), Dryden and Craig-Smith (2004), Forsyth *et al.* (2004) and Wilson and Reeder (2005). These data were supplemented with data collected from internet searches for non-indigenous ungulate species offered for hunting in countries globally, using country and species names as search terms in Google™ (www.google.com). The absence of a listing in any one of the above

publications or on the internet does not necessarily mean the species is absent from a country. However, in keeping with many macroecological studies it is assumed that absence data reflect real absences (the problems with this assumption and the need for making it have been widely discussed, see e.g. Gaston and Blackburn, 1999; Rondinini *et al.*, 2006). The relationship between the number of introductions and indigenous ungulate species-richness for countries globally was assessed using a Generalized Linear Model (Poisson distribution, log-link function), corrected for over-dispersion, implemented in Statistica 8.0 (StatSoft, Tulsa, Oklahoma).

Trends in ungulate introductions in South Africa

To investigate temporal trends in ungulate introductions in South Africa, data were compiled at a quarter-degree grid-cell (QDGC) resolution for indigenous species from Keith (2004) and for non-indigenous and extralimital ungulates from advertisements in *Landbou Weekblad* (Farmer's Weekly) magazine for all issues from 1965-2005 following the methods outlined in Chapter 2. All non-indigenous ungulate species included in the game and hunt sections of the classifieds of *Landbou Weekblad* were included in analyses. These data are assumed to be representative of species at a location based on their similarity with data in the literature (see Chapter 2) and the assumption that advertised species are established in the area.

New advertisements of extraregional species, extralimital species, and genetic variants and hybrids were summed, for each QDGC, for each year. Spearman's rank correlations were used to assess the relationship between the number of introductions and time. Temporal autocorrelation in the data were tested for by constructing correlograms using the autocorrelation function of time series analysis in Statistica 8.0 (StatSoft, Tulsa, Oklahoma). The statistical significance of temporal autocorrelation at $p < 0.05$ was tested for using the method of Oden (1984). Significant temporal autocorrelation was found in the extralimital and variant advertisement data. To assess the effect of temporal autocorrelation in the data the proportion of the data required to retain statistical significance was calculated. Due to the variation in range size (extent of occurrence) of ungulate species in South Africa, the area available for extralimital introductions in the country differs for each species, making direct comparisons of the number of extralimital introductions for each species inappropriate. As an alternative to direct comparisons of extralimital introductions a value of preference for

extralimital introduction was calculated for each species. Preference values were calculated as the number of QDGCs where the species has been advertised extralimitaly divided by the number of QDGCs available for extralimital introduction for each species.

Zoos as a pathway of ungulate introductions in South Africa

The transfer of non-indigenous species from zoos has been recorded as a route for ungulate introductions in various countries in the past (Lever, 1985; Long, 2003), and it appears that this phenomenon may be more widespread than previously appreciated (Chapter 2). To investigate the role of zoos as a pathway for or source of ungulate introductions in South Africa, zoo transfer reports from the International Species Information System (ISIS) (ISIS, 2007) were searched for non-indigenous ungulates that were sold or traded by South African zoological institutions. The number of non-indigenous ungulate species and individuals that were sold or traded from zoos in South Africa to other zoos, and to non-zoo recipients, were summed for each year from 1987 until 2006. A Mann-Whitney U test was used to determine whether significantly more non-indigenous ungulates were transferred from zoos to other zoos, or to elsewhere between 1987 and 2006.

Translocation distance

To determine the distances ungulates have been translocated in South Africa, two independent data sets were assessed. Penzhorn (1971) documented the re-introduction of ungulates into South African National Parks up to 31st December 1970. The coordinates of the National Parks and towns mentioned in the paper were used to estimate Euclidean distances of translocation using Shirokov's spherical law of cosines (Dale, 2005). Second, permit application data were obtained from CapeNature (Western Cape (provincial) nature conservation). The permit applications were for the translocation of ungulates into, within, and out of the Western Cape, South Africa, between March 2000 and August 2006. These data provide both the origin and destination municipality of the individual(s) to be translocated, so enabling the calculation of translocation distances and the construction of a dispersal kernel for the translocated species. The centroids of municipal districts were used to estimate the Euclidean distance of each translocation as above. Data from the eight other provincial authorities in South Africa were not readily accessible.

Impacts of ungulate introductions in South Africa

To assess documented, rather than hypothesised, impacts of ungulate introductions in South Africa, the literature was examined in two ways. First, the ISI Web of Science (1900 - 2007), Zoological Record (1864 – 2007), and Africa-Wide NiPAD (1900 - 2007) were searched using ungulate species names and “South Africa” as search terms, specifically searching for published work on competition, hybridisation, vegetation degradation, the introduction of new parasites and pathogens and any other impacts of ungulates introduced to South Africa. Second, the contents pages of the following South African publications (and their precursors) were browsed: *African Zoology* (1965 - 2007), *Annals of the Cape Provincial Museums* (1961 - 1997), *Annals of the South African Museums* (1898 - 2004), *Annals of the Eastern Cape Museums* (2000 - 2007), *Bontebok* (1981 - 1994), *Koedoe* (1958 - 2006), *Onderstepoort Journal of Veterinary Research* (1933 - 2007), *South African Journal of Wildlife Research* (1971 - 2007), *The Lammergeyer* (1971 - 2000), *Transvaal Museum Annals* (1962 - 1999), and a bibliography of the Natal Parks Board unpublished reports (1947-1998) (Sandwith, 2000). The reference lists of relevant papers were examined for additional literature that may have been overlooked during the first two searches. The impacts documented and the nature of the evidence provided was then recorded (for a similar approach see Parr & Chown, 2003).

Extent of range change

Methods for calculating range size and changes in range size have long been discussed (e.g. area of occupancy and extent of occurrence (EOO) – see Gaston, 1990; and the biases of minimum convex polygons – see Burgman & Fox, 2003). Moreover, to compare the results from this study with published information on range change as a result of climate change, a method comparable to that used in climate-induced range change modelling was required. For example Erasmus *et al.* (2002) calculated range size as the number of QDGCs suitable for occupation by a species in South Africa before and after predicted climate change (modelled using species presence data and climate data). Bearing these factors in mind, as well as data availability, the extents of range change as a result of translocations were calculated using four different methods. For method one, maps from Skinner and Chimimba (2005) were used to determine the full (Africa-wide) ‘historical’ EOO of the indigenous ungulate species, and extralimital advertisement data from *Landbou Weekblad* were then used to

calculate the extended EOO as minimum convex polygons. The distribution maps from Skinner and Chimimba (2005) were digitised using Landserf 2.2 (www.landserf.org) and converted into ArcGIS shape files using Gen2Shp (Wagner, 2002). The areas of each EOO were calculated in ArcMap 9.1 (ESRI, Redlands, California). Minimum convex polygons (MCPs) were created using the central points of QDGCs with extralimital advertisement data from *Landbou Weekblad* and the minimum convex polygon tool from Hawth tools (Beyer, 2004). Extended EOOs were taken as the area between the boundary of the 'historical' EOO and the extreme boundary of the MCP, clipping the MCP to the boundaries of South Africa. Change in distribution was calculated as a percentage increase in the EOO for each species. The remaining three methods used Keith (2004) as a source of 'historical' distribution data. Keith's (2004) data only provides distribution ranges (as EOO and presence in QDGCs – QDGC EOO) for South Africa, and not for the complete ranges of the species concerned. For method two, the number of QDGCs for each species in South Africa was counted, and the number of QDGCs with advertisement data was used to calculate the extended QDGC EOO. For method three the 'historical' EOO was calculated as a MCP using the central point of QDGCs in the QDGC data and the extended EOO was calculated using MCPs including *Landbou Weekblad* advertisement data. Lastly, for method four the 'historical' and extended EOOs of the ungulate species were calculated with Alpha hulls ($\alpha = 2$) (Mandal & Murthy, 1997) using the QDGC data from Keith (2004) and the *Landbou Weekblad* advertisement data. Alpha hulls use Delauney triangulation to determine areas bound by vertices shorter than α (Burgman & Fox, 2003). Alpha hulls were calculated using a customized program written in Mathematica 6.0 (Wolfram Research, Inc., Champaign, Illinois). Wilcoxon matched pairs tests (Conover, 1999) were used to compare the extent of occurrence before and after distribution changes as a result of translocations in all cases.

Areas of conservation concern

Due to concerns about potential ecological impacts (e.g. introgression and competition), introductions of extraregional, extralimital, genetic variant and hybrid ungulates in South Africa were designated here to constitute evidence of a potential conservation concern. Other forms of conservation threat included propagule pressure, which is a function of the number of individuals introduced and number of

introduction events (see Lockwood *et al.*, 2005 for discussion) and the introduction of non-indigenous species that can hybridise with indigenous species. For this analysis, extralimital species were defined as those species introduced outside their 'historical' extent of occurrence in South Africa as provided by Keith (2004) and extraregional species as those originating from outside the country.

Propagule pressure was calculated using extralimital species data from 1996 to 2005. Data were summed for each year a species was sold at a particular location (maximum value of 10 for each species). The relationship between propagule pressure and human population density and average annual income were also examined. It was assumed that propagule pressure might increase with human population density for two major reasons. First, because the probability of survival of the introduced animals is likely higher in favourable (high water and high energy) areas in South Africa (which would also mean higher indigenous ungulate species-richness – see Andrews & O'Brien 2000; Evans *et al.*, 2004 for rationale), and high energy areas support high human population densities (Chown *et al.*, 2003), the two variables might be related. Second, high human population density areas might also have a greater number of land owners able to afford the expense of ungulate purchases, in which case a relationship with average annual income might also be expected. Data to examine these hypotheses were obtained from Statistics South Africa (Statistics South Africa, 1996, 2001). The relationships between propagule pressure and human population size, average annual income and indigenous ungulate species-richness were examined using Generalized Linear Models (Poisson distribution, log-link function) correcting for over-dispersion. The Akaike Information Criterion was used to select the best model, with Akaike weight used to indicate the likelihood of a model being the best of the full set of models (Johnson & Omland, 2004).

QDGCs where introduced ungulates had potential to hybridise with indigenous species were identified. Only congeneric hybridisations were considered here, recalling that hybridisations are only problematic when they result in fertile offspring. Seven species pairs were considered, three of which included one extraregional species: black wildebeest, *Connochaetes gnou*, and blue wildebeest, *Connochaetes taurinus*, red hartebeest, *Alcelaphus caama*, and Lichtenstein's hartebeest, *Alcelaphus lichtensteinii*, common tsessebe *Damaliscus lunatus*, and bontebok, *Damaliscus*

pygargus, Burchell's zebra, *Equus burchellii*, and mountain zebra, *Equus zebra*, roan antelope, *Hippotragus equinus*, and sable antelope, *Hippotragus niger*, waterbuck, *Kobus ellipsiprymnus*, and lechwe, *Kobus leche*, scimitar-horned oryx, *Oryx dammah*, and gemsbok, *Oryx gazella*, and three sub-species pairs were also considered: Cape mountain zebra, *Equus zebra zebra*, and Hartmann's mountain zebra, *Equus zebra hartmannae*, bontebok, *D. pygargus pygargus*, and blesbok, *D. pygargus phillipsi*, and Cape eland, *Taurotragus oryx oryx*, and Livingstone's eland, *T. oryx livingstonii*. The subspecies designations used were referred to with specific vernacular names in *Landbou Weekblad*.

RESULTS

Trends and pathways

For countries to which ungulates have been introduced, no significant relationship was found between the number of introduced ungulates and indigenous ungulate species-richness ($\chi^2 = 1.97$, $p = 0.16$). South Africa was found to have introduced the second largest number of non-indigenous ungulates of any country globally, 38 compared to the U.S.A.'s 70 (Fig. 1).

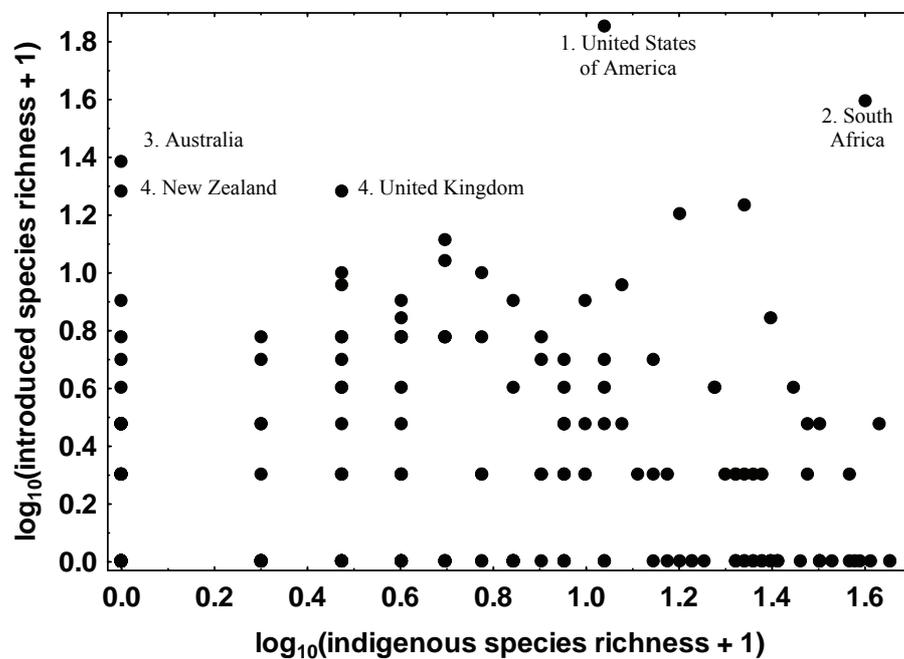


Figure 1. Non-indigenous ungulate introductions for countries globally in relation to the indigenous ungulate species richness of each country.

Advertisements were recorded for a total of 385 out of 1 816 QDGCs during the period 1965 to 2005. The number of advertisements for ungulate species increased through time between 1965 and 2005 (Fig. 2; extraregionals: Spearman's $R (r_s) = 0.29$, $p < 0.001$, with 34% of data $p = 0.047$; extralimitals: $r_s = 0.43$, $p < 0.001$, with 24% of data $p = 0.039$ and variants: $r_s = 0.57$, $p < 0.001$, with 20% of data $p = 0.031$).

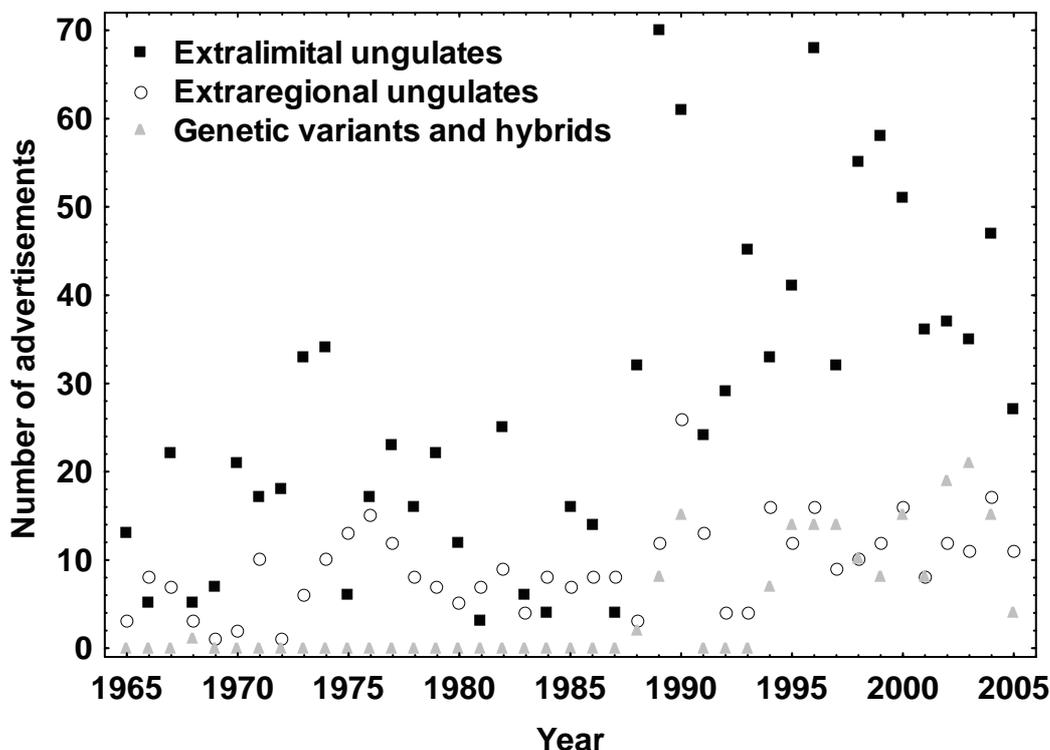


Figure 2. Number of new extraregional, extralimital and genetic variant and hybrid ungulate advertisements per quarter-degree grid-cell in South Africa, 1965-2005.

In total, the 18 extraregional ungulates (in 158 QDGCs) constituted 9% of advertisements. The most commonly advertised extraregional species were fallow deer, *Dama dama*, (98 QDGCs), water buffalo, *Bubalus bubalis*, (51 QDGCs), one-humped camel, *Camelus dromedarius*, (31 QDGCs), lechwe, *Kobus leche*, (28 QDGCs) and wild boar, *Sus scrofa*, (22 QDGCs). All indigenous ungulates were advertised for sale outside as well as inside their 'historical' distribution ranges and accounted for 55% of advertisements. Extralimital ungulates (in 264 QDGCs) comprised 31% of advertisements. The most preferred extralimital ungulates advertised were common eland, *Tragelaphus oryx*, gemsbok, *Oryx gazella*, blesbok, *Damaliscus pygargus phillipsi*, Burchell's zebra, *Equus burchellii*, and impala, *Aepyceros melampus*. A total of 14 different genetic variants and hybrids (in 83

QDGCs) comprised 5% of advertisements. The most widely sold variants were white blesbok, *D. pygargus phillipsi*, (31%), black springbok, *Antidorcas marsupialis*, (26%) and white springbok, *A. marsupialis* (17%).

Over the period 1987 to 2006, a total of 500 individuals of 19 non-indigenous ungulates were reported as sold or traded from zoos in South Africa to non-zoo recipients in South Africa (Fig. 3, no sales in 1987). More ungulate species (adjusted $Z = -3.63$, $p < 0.001$) and individuals (adjusted $Z = -4.47$, $p < 0.001$) were sold to non-zoo recipients than to zoo recipients.

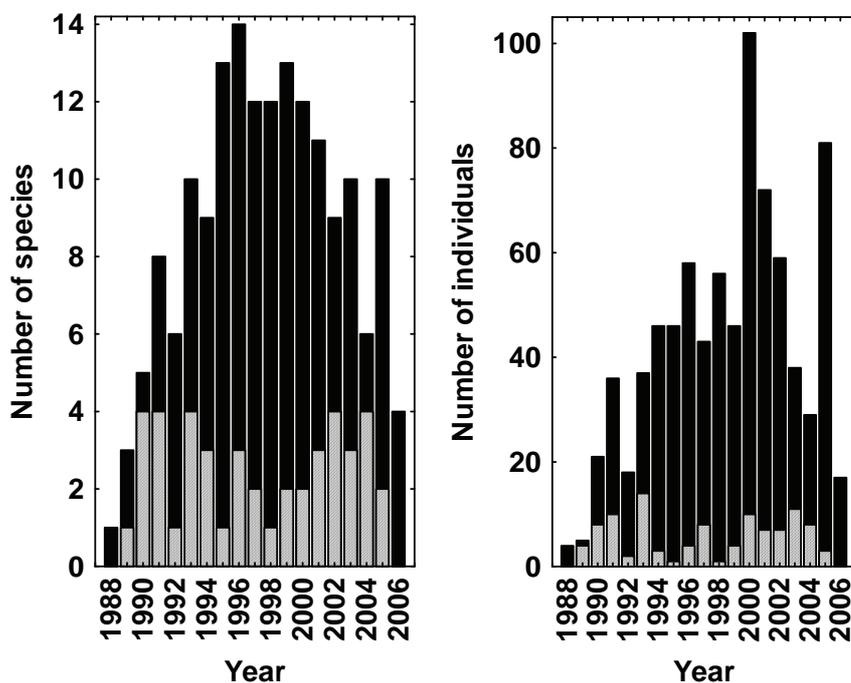


Figure 3. The number of non-indigenous ungulates sold or traded from zoos to other zoos (hatched bars) and to non-zoo recipients (solid bars) between 1988 and 2006, a) number of species and b) number of individuals.

For the 67 location-pairs from Penzhorn (1971) the mean Euclidean distance of translocation was 483 ± 287 km. For the 621 location-pairs from the CapeNature data the mean Euclidean distance of translocation was 490 ± 18 km (Fig. 4).

Impacts of ungulate introductions in South Africa

Few studies have clearly documented the impacts of ungulate introductions in South Africa. An unpublished study documented vegetation damage and soil erosion by

Himalayan tahr, *Hemitragus jemlahicus*, (P.H. Lloyd, 1975) and two unpublished reports document the diet of wild boar, *Sus scrofa*, and damage to agricultural areas and relatively untransformed habitat (J.H. Westdyk, 2000; D.L. Hignett, 2006). The most recent literature in South Africa largely concerns extralimital ungulates. One study reported anecdotal evidence of competition between bushbuck, *Tragelaphus scriptus*, and nyala, *Tragelaphus angasii* (Coates and Downs, 2005), whilst two others provided evidence of giraffe, *Giraffa camelopardalis* impacts on vegetation in its extralimital range (Bond and Loffell, 2001, Parker & Bernard, 2005). Two, largely inferential, studies have concerned hybridisation between subspecies or species (Fabricius *et al.*, 1989, 1988) and one study has concerned introgression (Grobler *et al.*, 2005). Inferences have also been made that the translocation of springbok, *A. marsupialis*, extralimitally introduced a lungworm (*Bronchonema magna*), which then infested bontebok, *Damaliscus pygargus pygargus*, (Meltzer, 1993). Finally, Braack *et al.* (1995) showed that non-indigenous parasite species such as the tick *Rhipicephalus maculatus* were introduced to the Kruger National Park with the reintroduction of ungulates from elsewhere in South Africa.

Extent of range change

Method one gave a mean increase in range size of 58 ± 16 %. When only using advertisement data from outside the species EOO the mean increase in range size for method two was 52 ± 49 % and when all advertisement data were used, including data from inside the species EOO a mean value of 117 ± 82 % was obtained. Method three gave a mean increase in range size of 159 ± 190 % and method four a mean increase in range size of 187 ± 191 % (Fig. 5). For all methods used the extent of occurrence differed significantly after the translocation of ungulates outside their 'historical' ranges in South Africa (each comparison gave the same result of: $Z = 4.372$, $p < 0.001$).

Areas of conservation concern

Propagule pressure was highest in densely populated areas (Table 1) and large areas of South Africa were categorized as areas of potential conservation concern due to ungulate introductions (Fig. 6). No significant relationships between propagule pressure and indigenous ungulate species-richness or average annual income were found (Table 1).

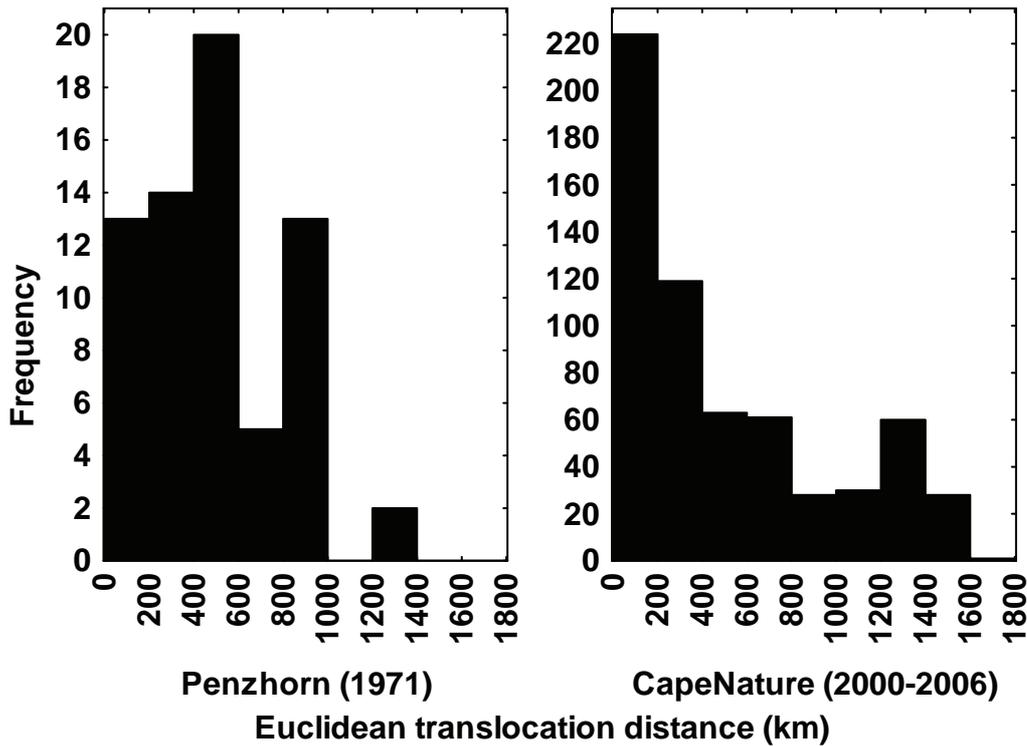


Figure 4. Frequencies of translocation distances calculated using data from Penzhorn (1971) on the re-introduction of ungulates to national parks (up until 1970) and translocation permit application data from CapeNature (2000 - 2006), both excluding translocations from outside the country.

DISCUSSION

Trends and pathways

Many countries globally have introduced large numbers of ungulates regardless of indigenous ungulate species-richness. South Africa is no exception and according to the available data has introduced more non-indigenous ungulates than any other country except the United States of America. Overall, the absence of a relationship between indigenous and introduced ungulate species-richness suggests that, at least on a geopolitical basis at the global scale, the 'rich get richer' hypothesis (Stohlgren *et al.*, 1999) does not apply to ungulate introductions. Rather, some countries are notable outliers to the mean number of species introduced. Nonetheless, the introduction of ungulates to a country is arguably the most significant first step of the process of invasion, and once introduced these species are likely to establish and spread, given enough time (Forsyth *et al.*, 2004; Jeschke & Strayer, 2005).

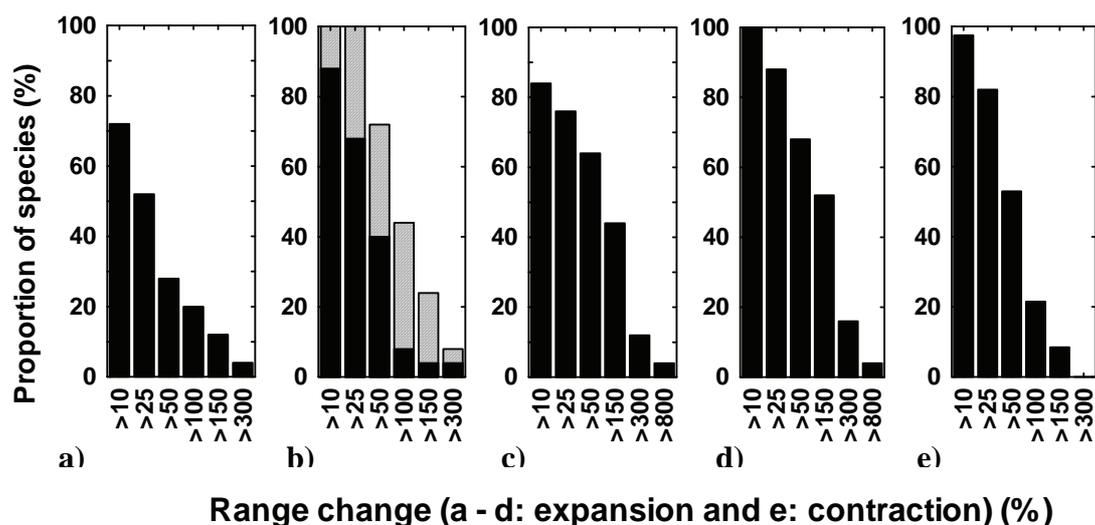
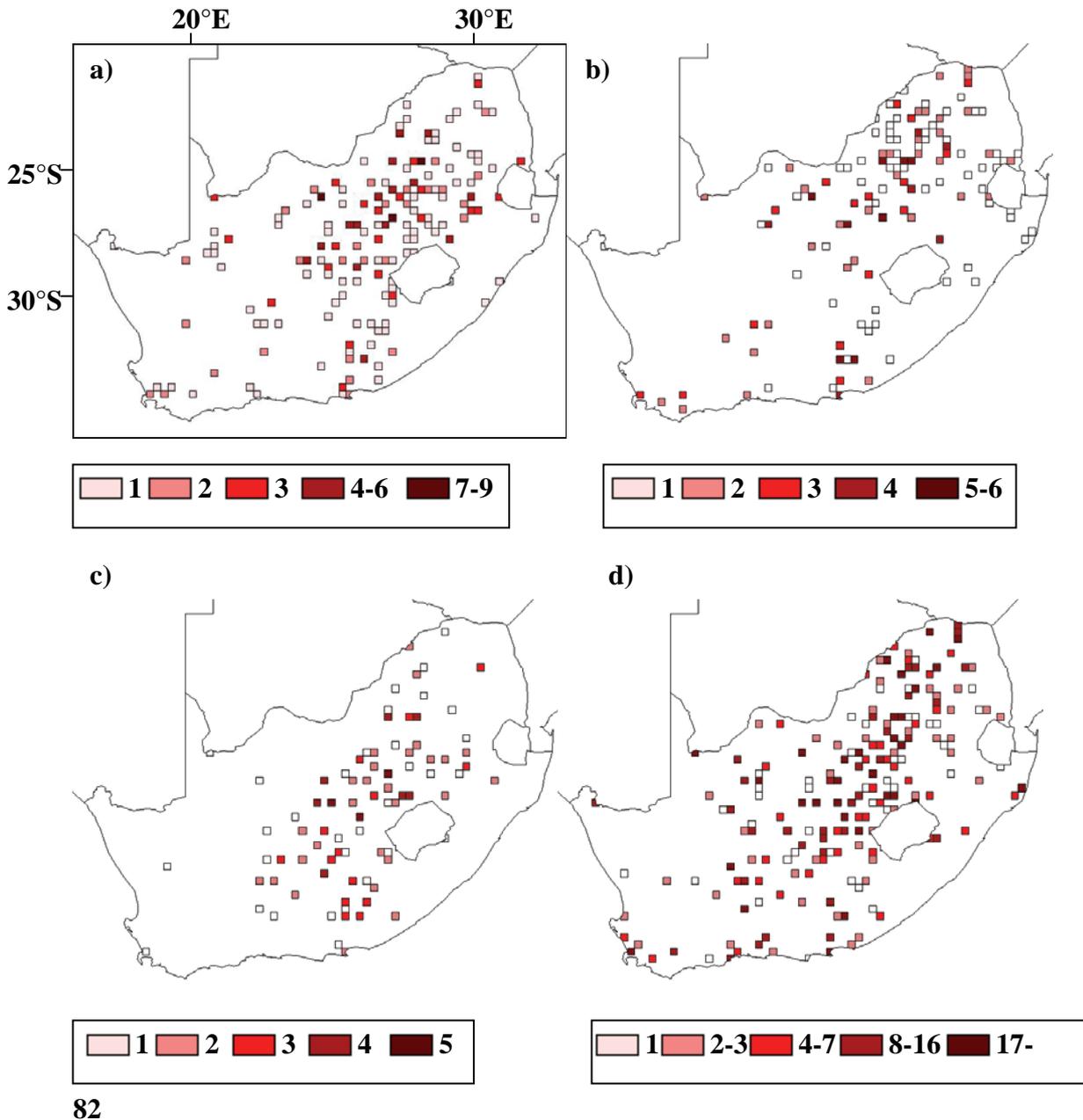


Figure 5. Percentage range expansion for 25 indigenous ungulate species as a result of translocations in South Africa (a-d) and predicted range contraction for different taxa in South Africa as a result of predicted climate change (e). a) Africa wide extent of occurrence (EOO) and extended EOO minimum convex polygons (MCPs), b) South African quarter-degree grid-cell EOO (QDGC EOO) and extended QDGC EOO recorded outside the species EOO (solid bars) as well as inside the species EOO (hatched bars). c) South African EOO MCPs and extended EOO MCPs, d) ‘Historical’ EOO and extended EOO calculated using Alpha hulls ($\alpha = 2$), e) Range contraction predicted as a result of predicted climate change for birds, mammals, reptiles and invertebrates in South Africa according to Erasmus *et al.* (2002).

Table 1. Generalized Linear Models (Poisson distribution, log-link function, correcting for over dispersion) for propagule pressure. Best subset models were selected using Akaike Information Criterion (AIC) and Akaike weights (w_i). The direction of relationship is in superscript for each predictor variable and non-significant relationships are indicated by NS. All maximum log likelihood ratio Chi-square (χ^2) results were significant at $p < 0.005$.

	AIC	w_i	χ^2
HUMAN POP ⁺ + INDIG ^{NS} + INCOME ^{NS}	3457	1.00	201
HUMAN POP ⁺ + INDIG ^{NS}	3468	0.00	188
HUMAN POP ⁺ + INCOME ^{NS}	3493	0.00	162

HUMAN POP: \log_{10} human population, INDIG: indigenous ungulate species-richness, INCOME: \log_{10} average annual income



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Figure 6. Areas of potential conservation concern in South Africa, in terms of a) the presence of extraregional ungulates, b) presence of potential hybrid ungulate pairs, c) presence of ungulate genetic variants and hybrids, and d) propagule pressure calculated from extralimital ungulate advertisements, 1996-2005 (maximum of 10 per extralimital ungulate per grid-cell).

Moreover, in this study it is also clear that once extraregional ungulates have been introduced, the numbers of new introductions increase through space and time (Fig. 2), suggesting that the likelihood of establishment of feral populations (i.e. those not subsidized or protected by human actions) will increase over time. Although several pathways for introductions clearly exist (e.g. directly from abroad to zoological gardens or private land owners – Lever, 1985; Long, 2003), ungulates that have been introduced to zoos in South Africa appear to have made their way from these institutions to private properties (e.g. Ross, 1997). Sales of non-indigenous ungulates from zoos to non-zoo recipients are common for other countries too (Chapter 2), and in some instances, non-indigenous ungulates such as Perè David's deer, *Elaphurus davidianus*, and scimitar-horned oryx, *Oryx dammah*, seem to have originated from endangered species breeding centres in South Africa (see Brand, 1980). In the United States limited space in zoos to house surplus animals may be part of the reason for extra-zoo sales (Lindburg, 1991; Lewandowski, 2003) and this may be the case here too.

Many of the introductions of non-indigenous species from zoos are likely to have been subject to a formal permitting process, and will clearly not necessarily lead to the establishment and spread of non-indigenous species especially in instances where, for example, only male individuals of a species were sold to a game farm (although this could have consequences for hybridisation). Moreover, where introduced ungulates have no substantive effect on indigenous species and ecosystems, the risks associated with sales to non-zoo recipients are likely to be low. Nonetheless, the release of non-indigenous species from ex-situ conservation institutions may be cause for at least some concern. If zoos have served as a pathway of introductions in the past their role could in some ways be compared with that of the aquarium and pet trades which serve as pathways for the introduction of fish (Rixon *et al.*, 2005; Weigle *et al.*, 2005), reptiles (Brown, 2006) and birds (Cassey *et al.*, 2004). In consequence, more attention needs to be given to relationships between the high value of zoos as facilities for ex-situ conservation and for the education of the public regarding the value of biodiversity (both mandated by the Convention on Biological Diversity (CBD) – Articles 9 and 13 (United Nations, 1993)) and the risks of their contribution to activities of conservation concern that should be minimized (CBD Articles 6, 7, 10, 14 (United Nations, 1993)).

Ungulate translocations in South Africa are not restricted to species from outside the country but include re-introductions of indigenous species and their translocation extralimitally, extending extents-of-occurrence of species in South Africa. The distances of translocations that have been undertaken by the game industry to and from the Western Cape in South Africa are similar to those undertaken to re-introduce species to National Parks in the country until the 1970s (Penzhorn, 1971). The fat tailed frequency distribution of ungulate translocations as shown by the permit application data not only indicates potential for a rapid rate of spread of ungulates in South Africa (see Trakhtenbrot *et al.*, 2005), but also considerable potential for genetic homogenization (see Olden *et al.*, 2004). In particular, the maximum distance of translocation was larger than the distance between the extremes of an average-sized geographic range (EOO) of an African ungulate (calculated using maps from Skinner and Chimimba, 2005). Maximum translocations were also further than long distance migrations undertaken by ungulates (see Berger, 2004). Whether these translocations have resulted in introgression, or will do so in future, depends on the specific translocation and whether it spans boundaries of evolutionary significance such as major rifts, rivers or uplift areas (see Arctander *et al.* (1999), Pitra *et al.* (2002) for information on such boundaries at the Africa-wide scale, and Moodley & Harley (2005) for an example from South Africa). The dispersal kernels calculated here indicate that introgression is likely for the maximum translocation distances because they are comparable to distances typically observed between significantly different populations of ungulates (e.g. see Arctander *et al.*, 1999; Lorenzen *et al.*, 2006). Thus, the distances that ungulates are being translocated in South Africa may have the potential to lead to genetic introgression, as has been found elsewhere (DeYoung *et al.*, 2003).

Having identified these risks, it should be noted that many early translocations (e.g. in the case of the movement of black rhinoceros, *Diceros bicornis*, from Kenya to the Addo Elephant park in the Eastern Cape of South Africa (Penzhorn 1971) – excluded from Fig. 4), were undertaken to lessen the risk of extinction for entire species, and other considerations were given lower priority in the face of substantial threat to the species as a whole (Griffith *et al.*, 1989). Modern conservation may be faced with similarly difficult decisions, but wherever possible consideration should be given to the extent to which translocations might cross boundaries of considerable

evolutionary significance. Not only might such introductions result in the loss of among-population diversity (see above and Storfer, 1999), but conservation actions are also only effective if they retain the potential for further evolutionary change in their target organisms and environments (Pressey *et al.*, 2003; Forest *et al.*, 2007).

In addition to the considerable translocation distances revealed by the current data, it is also found that some areas are characterized by considerable propagule pressure from extralimital species. Typically, these areas have higher human population densities than areas where propagule pressure is lower, but no relationship was found between average annual income and propagule pressure, and indigenous species-richness and propagule pressure. Thus, it seems that the major reason for high propagule pressure in high human density areas may have more to do with the probability of the survival (and perhaps reproduction) of the animals (see also Chown *et al.*, 2003; Evans *et al.*, 2006), than with factors such as economics. From an establishment perspective, these patterns of introduction may be self-reinforcing because high propagule pressure typically increases the likelihood that species will establish (Williamson, 1996; Forsyth & Duncan, 2001).

Realized impacts

As matters presently stand, the large increases in range sizes seen here are comparable with range alterations of c. 50 % or more, calculated by Erasmus *et al.* (2002) for different taxa in South Africa, Meynecke (2004) for vertebrates in northern Queensland in Australia and Lawler *et al.* (2006) for mammals in the western hemisphere, as a result of predicted climate change. The estimates of range change in this study are also larger than range changes of less than 20% calculated by Harrison *et al.* (2006) for mammals in Europe and Thuiller *et al.* (2006) for mammals in Africa estimated as a result of predicted climate change. Whilst considerable concern has been voiced about the impacts of climate change on species range positions and sizes (e.g. Parmesan, 2006), it is clear that for ungulates the magnitude of range alterations precipitated by humans can be much larger than those that are predicted to take place as climates change. Obviously, climate change frequently leads to range size reductions (e.g. Erasmus *et al.*, 2002; Thomas *et al.*, 2004), which is not the case here. Moreover, the landscape context of range changes, owing to interactions among landscape alteration, introductions and climate change, is also very different because

translocated individuals are moved to specific, often very favourable areas. Nonetheless, it should be recognized that direct human impacts on species distributions are often much larger than those forecast for the influence of climate change, and that they too may interact in ways that have not yet been sufficiently well explored.

Having identified the substantial translocation of ungulates to new areas, routes by which this might take place, and the potential for the development of conservation threats as a consequence of these translocations, the question remains of how much evidence exists to demonstrate that the potential threats are frequently realized. For South Africa, the answer is very little evidence. Despite arguments that introduced (extralimital or extraregional) ungulates may compete with their indigenous counterparts, only one study has attempted to demonstrate that this is the case (Coates & Downs, 2005), and the evidence presented is in the form of responses to questionnaires sent to managers of game reserves and farms regarding the status (i.e. increasing or decreasing population numbers) of bushbuck, *Tragelaphus scriptus*, and nyala, *T. angasii* on their properties. Demonstrations of competition typically require a more rigorous approach (see e.g. Gurevitch *et al.*, 1992). Quantification of vegetation impacts has likewise been uncommon, although Bond and Loffell (2001) provided comprehensive evidence that browsing by giraffe, *Giraffa camelopardalis* occurring extralimitally in savanna in KwaZulu-Natal, South Africa alters tree species distribution and composition. No studies have convincingly demonstrated introgression among species and/or subspecies of indigenous ungulates. Grobler *et al.* (2005) investigated introgression between blue wildebeest, *Connochaetes taurinus* and black wildebeest, *C. gnou*, but the outcome was not conclusive. Only Fabricius *et al.* (1988) have implied fertile F1 offspring from hybridisation between *C. taurinus* and *C. gnou* based on circumstantial, observational evidence. Demonstrations of impacts of introduced ungulates on foodwebs or on habitats are likewise slim. The impacts of *H. jemlahicus* and *S. scrofa* have been investigated in unpublished work from the Western Cape of South Africa, but little seems known of the impacts of commonly advertised species such as fallow deer, *Dama dama*, and lechwe, *Kobus leche*. However, *D. dama* have been reported to have spread into a provincial nature reserve in the Free State of South Africa, where they are continuously controlled through culling (Watson, 2006). Only one instance of host-switching among parasites

of wild ungulates in South Africa has been inferred (Meltzer, 1993) and no studies have demonstrated the transfer of disease between introduced and indigenous wild ungulates.

Lack of a demonstration of conservation problems caused by introductions does not mean that these do not exist. Indeed, elsewhere evidence for all of the above concerns has been recorded for ungulates (see Introduction). Moreover, there are good theoretical reasons to expect that such problems may arise (Gurevitch *et al.*, 1992; Cunningham, 1996; Rhymer & Simberloff, 1996). Clearly, many areas in South Africa could be subject to substantial impacts, given the extent of propagule pressure through introductions and translocations, and the numbers of species and individuals that are being marketed. Moreover, these areas are also those that have substantial numbers of indigenous ungulates, providing much potential for negative interactions. However, without evidence that the potential impacts of introductions are being realized, conservationists may be hard pressed to make a good case for limiting activities, such as ungulate introductions for trophy hunting and ecotourism purposes, that result in substantial economic benefit. Although it might be argued that a precautionary principle should be applied on the basis of work undertaken elsewhere and theoretical advances in conservation biology, an evidence-based approach (Sutherland *et al.*, 2004) will provide more efficient and convincing conservation decision-making (Pullin & Stewart, 2006).

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- Chapter IV -

Assessing surrogates of population genetic structuring to advise translocations

INTRODUCTION

Ungulates are one of the most extensively translocated taxa both within and between countries worldwide. Translocations have been undertaken for sport hunting (Griffith *et al.*, 1989; Matson *et al.*, 2004), to resolve human-animal conflict (Fischer & Lindenmayer, 2000) and for conservation purposes. They have also been used to reintroduce species to areas from which they were previously extirpated (Penzhorn, 1971; Griffith *et al.*, 1989) and to improve genetic diversity in small inbred populations (Moritz, 1999; Storfer, 1999). Most recently, translocations have been proposed as a means to restore functionality to ecosystems (Donlan, 2005; Zimov, 2005), and to assist the colonisation by populations of suitable habitats as climates change (Hoegh-Guldberg *et al.*, 2008). However, translocations undertaken for recreation or conservation purposes have raised concerns about genetic introgression (Greig, 1979; Slatkin, 1985, 1987; Avise, 1992; Storfer, 1999; Olden *et al.*, 2004). Indeed, inappropriate translocations have already led to introgression in squirrels (Hale *et al.*, 2004), fish (Vasemägi *et al.*, 2005; Eldridge & Naish, 2007) and rabbits (Delibes-Mateos *et al.*, 2008).

To prevent genetic introgression resulting from translocations it is essential to know the population genetic structure of each species (Riddle & Jones, 1996). This information is required to designate genetic units of conservation, such as Evolutionary Significant Units (ESUs) (Ryder, 1986), which are defined as groupings of individuals that are reciprocally monophyletic for mitochondrial DNA and show significant divergence of allele frequencies at nuclear loci (Moritz, 1994). ESUs represent the evolutionary history of species (Moritz, 1994) and are useful for identifying areas between which translocations should be prevented. However, the appropriate phylogeographic data required for designating such units of genetic distinctiveness are seldom available and the cost of obtaining these data limits the genetic management of species (Namkoong, 1996).

In the absence of phylogeographic data surrogates could provide a useful alternative to inform translocation decisions. To date, several surrogates for population genetic data have been proposed, including morphology (Hageman, 1995; Whittall *et al.*, 2004), subspecies designations (O'Brien & Mayr, 1991; Moritz, 2002; Phillimore & Owens, 2006), species diversity (Moritz, 2002), concentrations of endemic species (Moritz & Faith, 1998), and ecoregions (Moodley & Bruford, 2007). Other surrogates that might be useful are barriers to gene flow, because genetic structuring is often the result of vicariance following habitat fragmentation, or topography becoming a barrier after circumnavigation (Grubb, 1999). Indeed disjunct distributions (Friesen *et al.*, 2007), Pleistocene refugia (Hewitt, 2004; Zeisset & Beebee, 2008) and rivers and faults (Grubb, 1999; Cotterill, 2003; Zeisset & Beebee, 2008) have all been suggested as important in population genetic structuring.

Here the use of existing phylogeographic data, subspecies, ecoregions, disjunct distributions, rivers, faults and hypothesised Pleistocene refugia as surrogates for population genetic structure in African ungulates is assessed. Species diversity and concentrations of endemic species were not considered because these approaches have been deemed uninformative (Moritz & Faith, 1998; Moritz, 2002; but see Turpie & Crowe, 1994 for areas of endemism and variation in species diversity for African ungulates). The main rationale for this study is to provide a means to make informed decisions about proposed translocations in the absence of genetic data, such that conservation actions can be evidence-based (Pullin *et al.*, 2004; Sutherland *et al.*, 2004). Africa forms the primary focus of the study because more ungulates are found in Africa than on any other continent and they are translocated in large numbers over long distances for conservation (Penzhorn, 1971; Hearne & Swart, 1991; Munthali & Mkanda, 2002) and economic reasons (Castley *et al.*, 2001; Matson *et al.*, 2004; Loveridge *et al.*, 2006; Lindsey *et al.*, 2007).

For each of the surrogates assumptions need to be made about processes of divergence (these assumptions can be seen in Table 1).

Table 1. Assumptions made for the use of surrogates of population genetic structuring.

<p>Extrapolation of existing phylogeographic data</p> <p>I. Population genetic structuring reported by authors of phylogeographic studies represents actual population genetic structuring in the study species.</p> <p>II. Sympatric species show concordant phylogeographic patterns associated with zoogeographic barriers to gene-flow especially when they have responded in a similar way to geological or climatic events (Avice <i>et al.</i>, 1987; Avice, 1992; Riddle & Jones, 1996).</p>
<p>Subspecies</p> <p>I. Subspecies designations represent genetic distinctiveness in species (O'Brien & Mayr, 1991; Moritz, 2002; Phillimore & Owens, 2006).</p>
<p>Ecoregions</p> <p>I. Divergence is a consequence of natural selection on traits of organisms in different ecoregions (Miller, 1956; Endler, 1982; Schneider <i>et al.</i>, 1999; Schluter, 2001; Rundle & Nosil, 2005).</p>
<p>Disjunct distributions</p> <p>I. Populations diverge in isolation (Mayr, 1942, 1963; Futuyma & Mayer, 1980).</p>
<p>Rivers</p> <p>I. Rivers are a source of vicariance (Wallace, 1849; Wagner, 1868; Ayres & Clutton-Brock, 1992; Patton <i>et al.</i>, 1994; Moritz <i>et al.</i>, 2000).</p> <p>II. Rivers limiting species distributions now would have limited them for a considerable time into the past.</p> <p>III. Rivers that are old (were formed before species diverged), large (sufficiently wide) and stable are most likely to have caused vicariance.</p> <p>IV. Rivers that are proven to limit the movement of one ungulate species will limit other ungulate species (Avice <i>et al.</i>, 1987).</p>
<p>Faults</p> <p>I. Faults are a source of vicariance (Wallace, 1849; Chapman, 1917; Emsley, 1965; Cracraft & Prum, 1988; Ayres & Clutton-Brock, 1992; Heads, 1998).</p> <p>II, III and IV as for rivers (substitute 'Rivers' with 'Faults')</p>
<p>Hypothesised Pleistocene refugia</p> <p>I. Climatic and vegetational changes during the Cenozoic (deMenocal, 2004) led to genetic divergence in species (Forbes, 1846; Haffer, 1969; Mayr & O'Hara, 1986) because fauna and flora associated with particular habitats became isolated during habitat fragmentation (deMenocal, 2004).</p> <p>II. Locations of refugia correspond to phylogeographic sampling locations for species in studies, where genetic distinctiveness of sampled populations has been attributed to the existence of Pleistocene refugia.</p> <p>III. Locations of hypothesised refugia form the centre of the EOO of genetically distinct populations (Moritz <i>et al.</i>, 2000).</p>

To assess the utility of each surrogate, these assumptions (see Table 1) were considered, concordance between the surrogates and existing phylogeographic data was investigated, and the literature was searched for supporting information. Sister-species distributions were also used to indicate locations of barriers to gene-flow, as has previously been done (Benson *et al.*, 1962; Grubb, 1990). Recently, work on coral reef fish has demonstrated that biogeographic barriers identified using species distributions are fundamental in population genetic structuring (Rocha *et al.*, 2007). Sister-species distributions were used recognising that current geographic distributions are not always indicative of historical geographic distributions (Chesser & Zink, 1994; Gaston & Chown, 1999; Barraclough & Vogler, 2000; Losos & Glor, 2003).

METHODS

Phylogeographic structure

Phylogeographic studies on wild ungulate species (orders Artiodactyla and Perissodactyla) from around the world were examined to determine whether ungulates generally show population genetic structuring. The ISI Web of Science was searched using ungulate species names and the following search terms: ‘genetic variability’, ‘genetic diversity’, ‘phylogenetic’, ‘phylogeography’, ‘population structure’ and ‘population differentiation’. The reference lists of all papers were examined to determine whether further papers had been missed. The collated papers were checked to determine whether the authors concluded significant population genetic structuring had been found based on monophyly of mtDNA or significant divergence of allele frequencies of nuclear or mitochondrial DNA.

For the remainder of the study, only phylogeographic studies on African ungulates were used. To examine the extent of sampling of these studies the mean and standard error of the number of individuals and sites sampled for each species was calculated. The number of studies for which at least one population satisfied the requirements for designation as an ESU (reciprocal monophyly for mtDNA and significant divergence of allele frequencies) were counted. To determine overlap in sampling sites for different species, a species-area matrix, of the areas that have been sampled for the different species, was constructed (see Brooks *et al.*, 2001) and the proportion of

overlap between areas sampled was calculated. To identify patterns in population structuring area cladograms were constructed for each species (see Brooks *et al.*, 2001). Broad regional areas such as southern Africa, eastern Africa, south-western Africa and west Africa were used because authors commonly group populations by these areas. The number of investigations documenting divergence between the same regions was enumerated and reported.

To illustrate the geographical extent of sampling and patterns in population genetic structuring for African ungulate species, the extent-of-occurrence (EOO) of each species and sampling sites were mapped in ArcMap 9.1 (ESRI, Redlands, California). All subsequent mapping was conducted in ArcMap 9.1 (ESRI, Redlands, California). EOO maps were obtained from the African Mammal Databank (AMD) (IEA, 1998) and coordinates for the sampling sites cited in phylogeographic studies were obtained from the text of studies or by searching www.fallingrain.com/world/ and www.earthsearch.net using sampling site names. Sampling sites for each species were grouped into significantly different populations based on the groupings used by the authors of the phylogeographic studies.

Subspecies

The number of recognised subspecies according to Wilson & Reeder (2005) was recorded for each species and the mean and standard error of the number of subspecies per ungulate species in Africa (96 in total) was calculated. The proportion of subspecies sampled for each species was calculated using the number of subspecies recognised by the author of each study. A mean, standard error and 97% confidence interval of the proportion of subspecies sampled was then calculated. Phylogeographic studies were examined for whether the authors considered that they had found support for the subspecies they had sampled using mitochondrial DNA. When using monophyly of haplotype groups as a criterion for support, some authors made exceptions to complete monophyly and accepted the presence of one ‘foreign’ haplotype in a clade, and their decisions were accepted for this investigation. The proportion of studies for which authors reported support for all subspecies sampled was calculated. To incorporate studies that found only partial support for the subspecies examined, the number of subspecies supported by monophyly was counted

and expressed as a proportion of the total number of subspecies examined in each study. A mean and standard error was then calculated for these proportions.

Ecoregions

To determine the mean and standard error of the number of ecoregions and biomes per ungulate species in Africa the ecoregions and biomes encompassed by the EOO of each African ungulate species were assessed. To do this the ecoregion map of Olson *et al.* (2001) was first clipped by the EOO of each ungulate species. Ecoregions that are considered unsuitable according to species datasheets in the African Mammal Databank (IEA, 1998) were excluded and the number of remaining suitable ecoregions and biomes were counted for each species. To assess whether ecoregion and biome designations correspond to existing phylogeographic data, the sampling sites of phylogeographic studies were first mapped with the ecoregions and biomes (Olson *et al.*, 2001), and each sampling site was assigned to the ecoregion and biome that encompasses it. Then the proportion of ecoregions and biomes that were supported by monophyly were calculated for each species. A mean, standard error and 95% confidence interval was then calculated for these proportions for both ecoregions and biomes.

Disjunct distributions

Disjunct range fragments were defined as range fragments that are more than 200 km apart. This distance was chosen as a conservative estimate of the distance between habitat fragments that causes isolation between populations and it considers the maximum distances ungulates migrate (see Berger, 2004). The number of range fragments was counted for each African ungulate species by mapping the EOO for each ungulate species and measuring the distance between range fragments. The EOO of allopatric sister-species and species, with disjunct distributions, were overlaid and overlapping distribution patterns were noted. The utility of disjunct species distributions as a surrogate for population genetic structuring was assessed based on whether disjunct species distributions were supported by monophyly in phylogeographic studies. For species with disjunct distributions and existing phylogeographic data, populations were assigned to different range fragments. The number of range fragments supported by monophyly was counted and expressed as a

proportion of the total number of range fragments examined in each study. A mean, standard error and 95% confidence interval was then calculated for these proportions.

Rivers

The number of African ungulate species whose ranges are dissected by rivers was counted by mapping the EOO of each African ungulate species with major rivers (Strahler stream order 5 and above). Global river data were obtained from the United States Geological Survey (<http://education.usgs.gov/common/lessons/africa.html>). Molecular support for major rivers as sources of vicariance was assessed by determining whether rivers dissected species ranges in such a way that the populations on either side of a river form monophyletic groups. A mean, standard error and 95% confidence interval was calculated for the proportion of species for which this was the case.

To investigate the relationship between rivers and sister-species distributions, rivers were mapped with the EOO of sister-species pairs. Sister-species were designated using the phylogeny of Hernández Fernández & Vrba (2005). For sister-species that showed parapatric distributions the area of contact between the two species' ranges was examined for the existence of a river. Individual African ungulate species were also mapped to examine the number of species whose distributions are limited by major rivers. The literature was searched for examples of rivers acting as barriers or causing vicariance in African fauna.

Faults

The number of African ungulate species whose ranges are dissected by fault lines was counted by mapping the EOO of each African ungulate species with fault lines. Global fault line data were obtained from the United States Geological Survey (<http://education.usgs.gov/common/lessons/africa.html>). Molecular support for faults as sources of vicariance was assessed by determining whether faults dissected species ranges in such a way that the populations on either side of a fault form monophyletic groups. A mean, standard error and 95% confidence interval was calculated for the proportion of species for which this was the case.

To investigate the relationship between faults and sister-species distributions faults were mapped with the EOO of sister-species pairs. For sister-species that showed parapatric distributions, the area of contact between the two species' ranges was examined for the existence of a fault. Individual African ungulate species were also mapped to examine the number of species whose distributions are limited by faults. The literature was searched for examples of faults acting as barriers or causing vicariance in African fauna.

Pleistocene refugia

The literature was searched for studies that hypothesised Pleistocene refugia for ungulates species. Locations of hypothesised Pleistocene refugia were mapped based on the sampling sites of populations whose genetic distinctiveness was attributed to Pleistocene refugia. The geographical extent of influence of Pleistocene refugia could not be defined and therefore no further analyses were performed.

Comparing the surrogates

To compare the spatial scale of the surrogates the mean number of surrogate units per ungulate species was compared using the GT2 test (Sokal & Rohlf, 1997). For ungulate species with existing phylogeographic data the mean proportion of surrogate units per species that were supported by monophyly were compared using the GT2 test (Sokal & Rohlf, 1997). The main patterns demonstrated by each of the surrogates were overlaid to examine overlap.

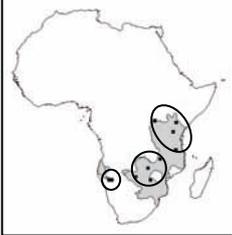
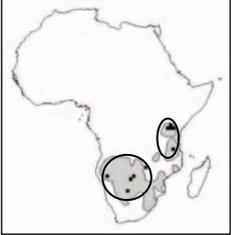
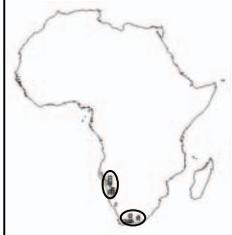
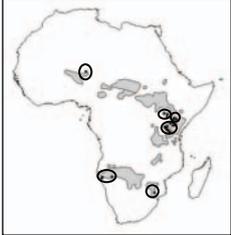
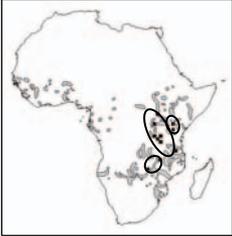
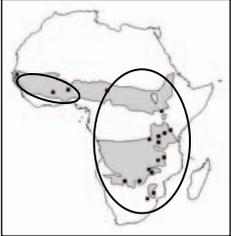
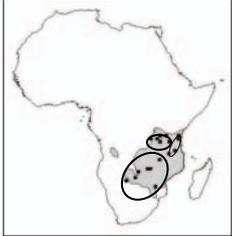
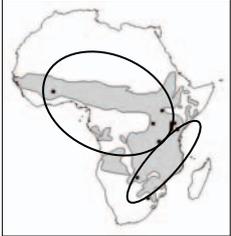
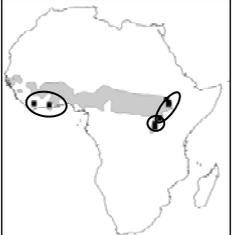
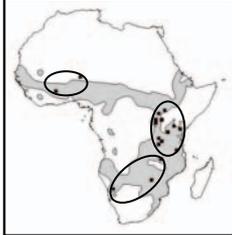
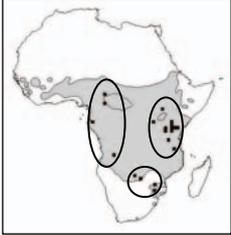
RESULTS

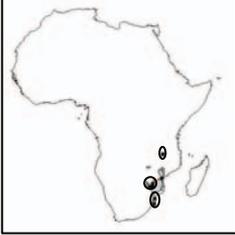
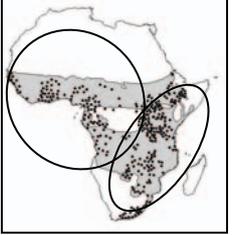
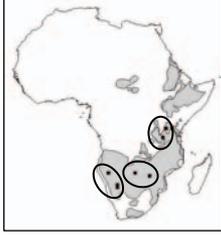
Phylogeographic structure

Of the 51 ungulate species from around the world, for which phylogeographic studies were found (20 % of the global ungulate fauna of 255 species), 40 species showed significant population genetic structuring (Table 1 in Appendix). Of the 96 African ungulate species, phylogeographic data were only available for 15 species. The number of sites sampled did not cover the full distribution ranges of the species, except for *T. scriptus* (Fig. 1). Excluding the extensive study of *T. scriptus*, the mean number of sites sampled was 15.4 ± 1.47 and the mean number of individuals sampled was 150 ± 23.7 (Table 2). Of the 15 species with phylogeographic data ESUs were

only demonstrated for two species. The areas sampled for the 15 different species overlapped by 47.8%.

Figure 1. Population genetic structuring in African ungulate species showing extent of occurrence, sampling sites of molecular studies and groupings of genetic distinctiveness as suggested by the authors of phylogeographic studies.

<p><i>Aepyceros melampus</i></p>  <p>Lorenzen <i>et al.</i>, 2006a*</p>	<p><i>Connochaetes taurinus</i></p>  <p>Arctander <i>et al.</i>, 1999</p>	<p><i>Equus zebra</i></p>  <p>Moodley & Harley, 2005</p>	<p><i>Giraffa camelopardis</i></p>  <p>Brown <i>et al.</i>, 2007</p>
<p><i>Hippopotamus amphibius</i></p>  <p>Okello, 2005</p>	<p><i>Hippotragus equinus</i></p>  <p>Alpers <i>et al.</i>, 2004**</p>	<p><i>Hippotragus niger</i></p>  <p>Pitra <i>et al.</i>, 2002**</p>	<p><i>Kobus ellipsiprymnus</i></p>  <p>Lorenzen <i>et al.</i>, 2006b</p>
<p><i>Kobus kob</i></p>  <p>Lorenzen <i>et al.</i>, 2007</p>	<p><i>Nanger granti</i></p>  <p>Lorenzen <i>et al.</i>, 2008</p>	<p><i>Phacochoerus africanus</i></p>  <p>Muwanika <i>et al.</i>, 2003</p>	<p><i>Synceros caffer</i></p>  <p>van Hooft <i>et al.</i>, 2002</p>

<p><i>Tragelaphus angasii</i></p>  <p>Grobler <i>et al.</i>, 2005</p>	<p><i>Tragelaphus scriptus</i></p>  <p>Moodley & Bruford, 2007</p>	<p><i>Tragelaphus strepsiceros</i></p>  <p>Nersting & Arctander, 2001</p>	
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* also see Nersting & Arctander, 2001; ** also see Mathee & Robinson 1999

Table 2. Molecular studies of population genetic structuring in African ungulate species: extent of sampling, support for subspecies and population structuring. For all species significant population structuring was found; Y, yes; N, no; S, some; n.a., not applicable; AU, authors

Species	sampling		subspecies		mtDNA control region				microsatellites			References
	n sites	n subspp.	Total n subspp. recognised by AU	sub spp. supported	n individuals	n base pairs	n haplotypes	reciprocal monophyletic grouping	n individuals	n microsat loci	significant divergence of allele frequencies	
<i>Aepyceros melampus</i>	19	2	2	Y	155	400	106	N	162	8	Y	Nersting & Arctander, 2001
<i>Connochaetes taurinus</i>	11	5	5	N	123	388	96	N	n.a	n.a	N	Lorenzen <i>et al.</i> , 2006a
<i>Equus zebra</i>	10	2	2	Y	77	445	28	N	291	15	Y	Arctander <i>et al.</i> , 1999
<i>Giraffa camelopardalis</i>	19	5	9	Y	266	654	>35	Y	381	14	Y	Moodley & Harley, 2005
<i>Hippopotamus amphibious</i>	13	3	5	Y	109	400	100	N	n.a	n.a	n.a	Brown <i>et al.</i> , 2007
<i>Hippotragus equinus</i>	18	5	6	S	137	401	52	Y	137	8	Y	Okello, 2005
<i>Hippotragus niger</i>	17	3	4	S	95	492	50	Y	n.a	n.a	n.a	Alpers <i>et al.</i> , 2004
<i>Kobus ellipsiprymnus</i>	11	2	2	Y	173	478	88	N	116	14	Y	Pitra <i>et al.</i> , 2002
<i>Kobus kob</i>	10	3	3	N	187	357	90	N	151	7	Y	Lorenzen <i>et al.</i> , 2006b
<i>Nanger granti</i>	17	4	4	N	117	375	129	Y	n.a	n.a	n.a	Lorenzen <i>et al.</i> , 2007
<i>Phacochoerus africanus</i>	24	2	4	Y	181	370	70	N	143	6	Y	Lorenzen <i>et al.</i> , 2008
<i>Syncerus caffer</i>	23	3	3	S	381	351	124	N	73	1	S	Muwanika <i>et al.</i> , 2003
<i>Tragelaphus angasii</i>	5	n.a.	n.a.	n.a.	19	519	?	N	33	3	Y	van Hooft <i>et al.</i> , 2002
<i>Tragelaphus scriptus</i>	239	33	33	Y	485	516	320	Y	n.a	n.a	n.a	Grobler <i>et al.</i> , 2005
<i>Tragelaphus strepsiceros</i>	19	2	3	n.a	90	400	46	Y	n.a	n.a	n.a	Moodley & Bruford, 2007
												Nersting & Arctander, 2001

Seven species showed divergence between eastern and southern Africa, three species showed divergence between eastern and western Africa, two species showed divergence between south-western Africa and southern Africa and the other species showed more complicated phylogeographic patterns (Fig. 1).

Subspecies

The mean number of subspecies per ungulate species in Africa, according to Wilson & Reeder (2005) is 2.64 ± 0.30 (Fig. 2). Forty African ungulate species, most with ranges under 1 000 000 km², have no subspecies recorded in Wilson & Reeder (2005). The phylogeographic studies sampled 85.0 ± 5.22 % of the subspecies recognised by the authors of each study (Table 2), these subspecies designations corresponded to population genetic structuring for 53.8 % of the species (see Table 2) and a mean of 56.1 ± 13.5 % of the subspecies assessed for each species were supported by monophyly (Fig. 2).

Ecoregions

The mean number of ecoregions and biomes per African ungulate species is 16.4 ± 1.52 and 2.76 ± 0.12 , respectively and the mean number of ecoregions and biomes supported by monophyly for each species was 13.8 ± 4.66 % and 5.00 ± 5.00 % respectively (Fig. 2).

Disjunct distributions

African ungulate species' ranges are generally not disjunct (mean number of range fragments > 200 km apart: 0.88 ± 0.15 (Fig. 2)). According to the African Mammal Databank, 63 African ungulate species have continuous EOs. Of the four species with phylogeographic data and disjunct distributions three species formed monophyletic clades that corresponded to range fragments (Fig. 2). The correspondence of disjunct species distributions with population genetic structuring can be seen in Fig. 1 for *Equus zebra* and to a lesser degree for *Connochaetes taurinus*. Disjunct distribution patterns overlapped for three species (*Madoqua kirkii*, *Redunca fulvorufula* and *Raphicerus campestris*) and three sister-species pairs (*Oryx gazella* and *O. beisa*, *Tragelaphus angasii* and *T. imberbis* and *Ammodorcas clarkei* and *Antidorcas marsupialis*) (see Fig. 1 in Appendix & Fig. 3).

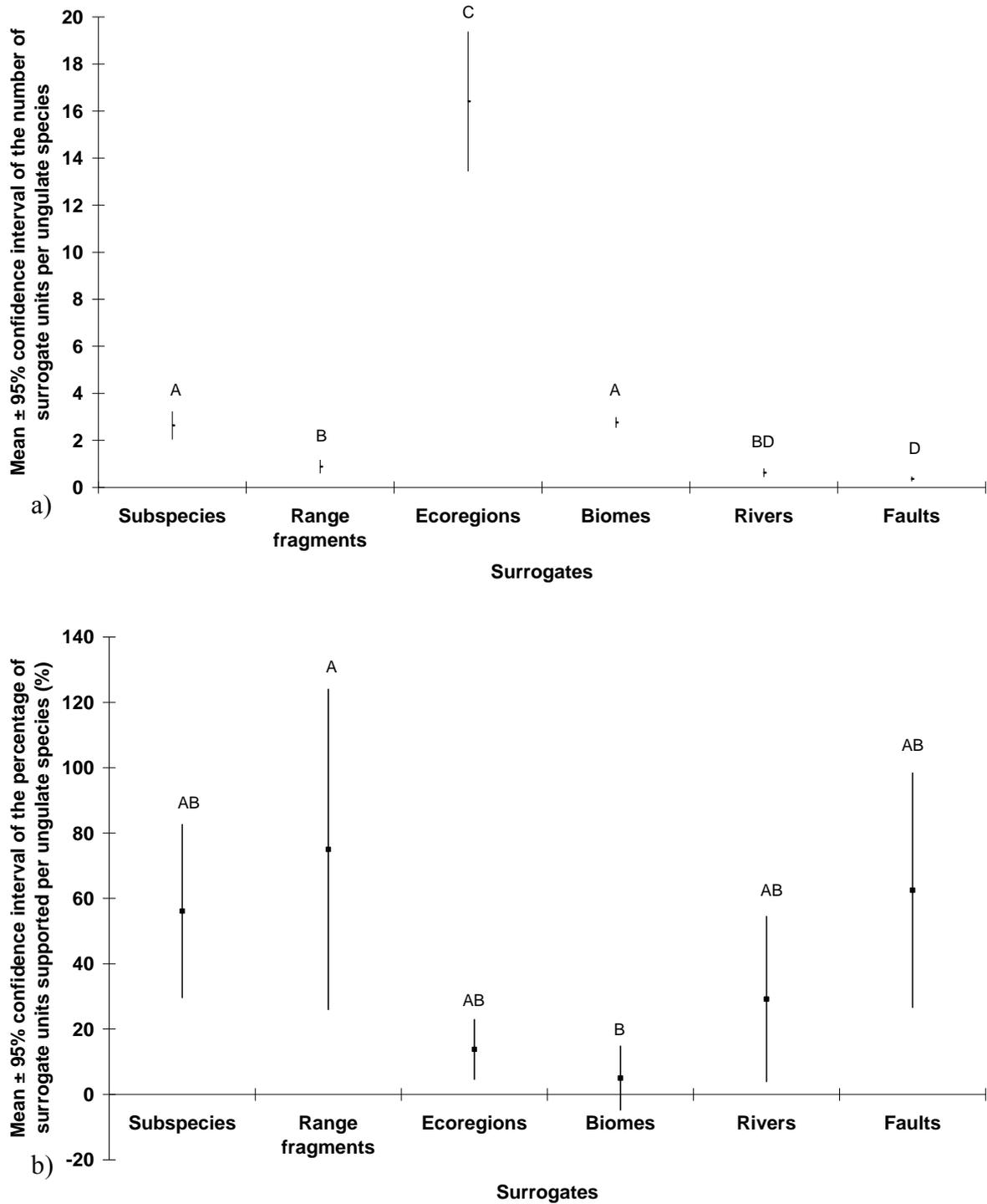


Figure 2. The utility of surrogates of genetic distinctiveness in African ungulate species: a) the mean number of surrogate units per species and b) the mean number of surrogate units supported by phylogeographic data for each species. Means with different letters are significantly different (at $p < 0.05$) according to the GT2 test.

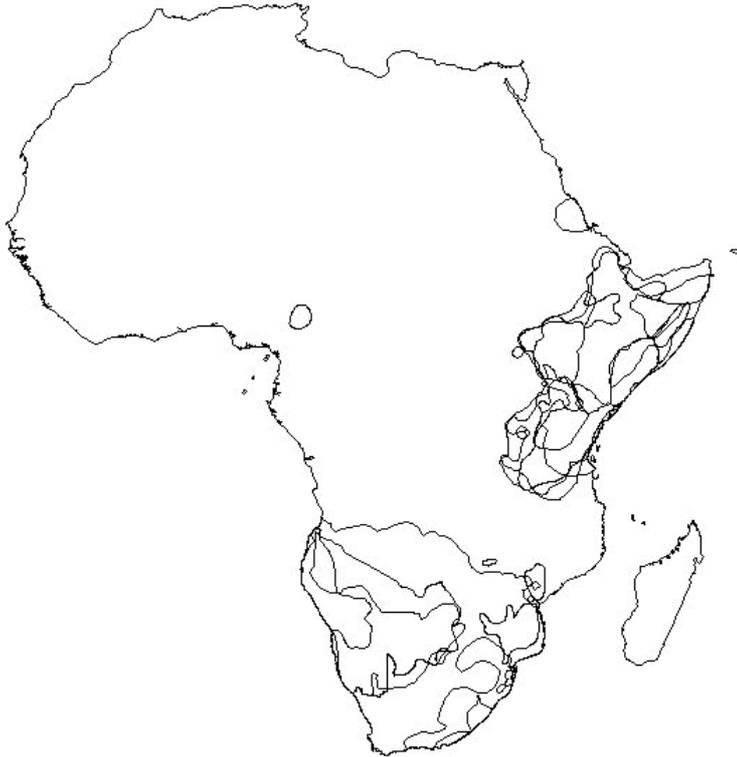


Figure 3. Disjunct distributions of ungulate species (*Madoqua kirkii*, *Redunca fulvorufula* and *Raphicerus campestris*) and sister-species (*Oryx gazella* & *Oryx beisa*, *Tragelaphus angasii* & *Tragelaphus imberbis* and *Ammodorcas clarkei* & *Antidorcas marsupialis*).

Rivers

Rivers of stream order 5 and above dissect the EOO of 36 African ungulate species (Fig. 2). The Niger river dissects the largest number of species' EOOs (20) followed by the Nile river (15), Congo drainage system (10), Zambezi river (13), Orange river (1) and Limpopo river (1). Existing phylogeographic data on ungulates are distributed across major rivers in nine cases and monophyly is found on either side of the Niger river one out of two times, the Orange river once, and the Zambezi river only one out of six times. Consequently, the mean number of population groupings, on either side of major rivers that were supported by monophyly was 29.2 ± 12.9 % (Fig. 2). Major African rivers, specifically the Nile, Niger and Congo rivers also separate sister-species distributions (Table 3) and limit species distributions. The Congo river and tributaries limit the EOOs of the most ungulate species (8) and the limitation of species ranges also corresponds to a change in biomes on either side of the river.

Table 3. Rivers as surrogates for delineating population genetic structuring in ungulate species in Africa.

a) Evidence from ungulate species

Evidence	River(s)	Taxa	References
SIS P	Nile	<i>Taurotragus oryx</i> & <i>T. derbianus</i> <i>Nanger dama</i> & <i>Nanger soemmerringii</i>	This study
SIS P	Congo	<i>Cephalophus rufilatus</i> & <i>C. nigrifrons</i> <i>C. callipygus</i> & <i>C. weynsi</i>	This study
SIS P	Niger	<i>Philantomba maxwelli</i> & <i>P. monticola</i>	This study
SDR	Zambezi	<i>Giraffa camelopardalis</i>	Cotterill, 2003
SDR	Niger & Volta	<i>Artiodactyla</i>	Booth, 1958
SBD	Zambezi	<i>Conchaetes taurinus</i>	Cotterill, 2003
SUS S	Cunene	<i>Aepyceros melampus</i>	Cotterill, 2003

b) Evidence from other taxa

SDR	Congo & Oubangui	<i>Hylomyscus alleni</i> & <i>H. stella</i>	Booth, 1958
SDR	Niger & Volta	Sciuromorpha	Booth, 1958
SDR	Cross & Sanaga	Mammals	Happold, 1996
SDR	Congo, Oubangui, Volta & Niger	<i>Hylochromus</i>	Nicolas <i>et al.</i> , 2006
SDR	Limpopo, Zambezi, Luangwa, Nyasa & Shire	Aves	Benson <i>et al.</i> , 1962
SDR	Limpopo & Zambezi	Plants	Moore, 1988
SDR	Niger & Volta	Mammals	Robbins, 1978
SUS/SIS S	Limpopo, Zambezi, Luangwa, Nyasa & Shire	Aves	Benson <i>et al.</i> , 1962
SUS/SIS S	Sanaga, Congo, Kasai, Sassandra, Niger	Primates	Grubb, 1990
PS	Congo basin	<i>Pan paniscus</i>	Eriksson <i>et al.</i> , 2004
PS	Congo, Cross, Sanaga, Ogooué, Ivindo, Sangha & Ubanguui	<i>Gorilla gorilla</i>	Anthony <i>et al.</i> , 2007

PS, population structuring across river; SBD, species break in distribution across river; SDR, species distribution restricted by river; SIS P, sister-species parapatric across river; SIS S, sister-species separated by river; SUS S, subspecies separated by river.

Faults

The EOO of 31 ungulate species are divided by faults and the EOO of 15 species are restricted by faults. The mean number of population groupings, on either side of the Gregory or East African rift, that were supported by monophyly was 62.5 ± 18.3 % (Fig. 2). The location of the east African rift valley and Gregory rift also correspond with the separation of sister-species, subspecies and the fragmentation of geographic distributions of ungulates and other taxa (Fig. 1; Table 4).

Pleistocene refugia

Pleistocene refugia in south-western Africa (Nersting & Arctander, 2001), southern Africa (Arctander *et al.*, 1999; Muwanika *et al.*, 2003; Lorenzen *et al.*, 2006a), eastern Africa (Muwanika *et al.*, 2003; Alpers *et al.*, 2004; Okello *et al.*, 2005; Lorenzen *et al.*, 2007) and western Africa (Muwanika *et al.*, 2003; Alpers *et al.*, 2004; Lorenzen *et al.*, 2006a, 2007) have been hypothesised for ungulate species and are often used to explain patterns seen in population genetic structuring (see Fig. 4 for approximate locations).

Comparing the surrogates

Spatial scale differed between many of the surrogates (Fig. 2a). The large number of ecoregions that are encompassed by each species EOO made the spatial scale of this surrogate particularly different from the rest of the surrogates (Fig. 2a). However, the percentage of molecular support for each of the surrogates was not significantly different (Fig. 2b) even though some of the surrogates, e.g. faults, had a larger percentage of surrogate units supported by phylogeographic data. Some of the surrogates showed similar patterns when overlaid. For example, disjunct distributions resemble patterns shown by the phylogeographic data for other ungulate species, and for separation by the east African rift valley (Fig. 4). Locations of hypothesised Pleistocene refugia largely mirror patterns in phylogeographic data, as these refugia were hypothesised as an explanation of those very phylogeographic patterns.

Table 4. Faults (and associated topology, climate and vegetation) as surrogates for delineating population structuring in ungulate species in Africa.

a) Evidence from ungulate species

Evidence	Barrier	Taxa	References
SIS S	East African rift	<i>Phacochoerus aethiopicus</i> & <i>P. africanus</i> <i>Neotragus batesi</i> & <i>N. moschatus</i>	This study
SUS S/ SD	Gregory rift	<i>Kobus ellipsyprimus</i>	Lorenzen <i>et al.</i> , 2006b
SUS S	Muchinga escarpment	<i>Kobus ellipsyprimus</i>	Cotterill, 2003
SUS S/ PS	Rift valley axis	<i>Tragelaphus scriptus</i>	Moodley & Bruford, 2007
PS	Gregory rift	<i>Tragelaphus scriptus</i>	
PS	East African rift	<i>Connochaetes taurinus</i>	Arctander <i>et al.</i> , 1999
		<i>Aepyceros melampus</i>	Templeton & Georgiadis, 1995
	rift valley	<i>Hippotragus equinus</i>	Matthee & Robinson, 1999
		<i>Hippotragus niger</i>	Pitra <i>et al.</i> , 2002
		<i>Giraffa camelopardalis</i>	Brown <i>et al.</i> , 2007
SBD	Muchinga escarpment	<i>Kobus vardonii</i> <i>Kobus leche</i> <i>Hippotragus niger</i>	Cotterill, 2003

b) Evidence from other taxa

SD	East African rift	Bathergidae	Faulkes <i>et al.</i> , 2004
PS	East African rift	<i>Theropithecus gelada</i> <i>Struthio camelus</i> <i>Lycaon pictus</i> <i>Pedetes capensis</i>	Belay & Mori, 2006 Freitag & Robinson, 1993 Girman <i>et al.</i> , 1993 Matthee & Robinson, 1997
SDF	Muchinga escarpment	Mammals	Ansell, 1960, 1978
SIS S	Muchinga escarpment	<i>Helioscirus gambianus</i> & <i>H. mutabalis</i>	Cotterill, 2003
SDR	Luangwa and Shire/Nyasa rifts	Aves	Benson <i>et al.</i> , 1962
SIS / SUS S	Luangwa, Shire/Nyasa & Kenya rifts	Aves	Benson <i>et al.</i> , 1962
CZA	East African rift	Mammals	Grubb, 1999

CZA, contact zones of allotaxa; PS, population structuring across rift; SBD, species break in distribution across rift; SD, species divergence; SDF, species distribution fragmented across rift; SDR, Species distribution restricted by rift; SIS P, sister-species parapatric across rift; SIS S, sister-species separated by rift; SUS S, subspecies separated by rift.

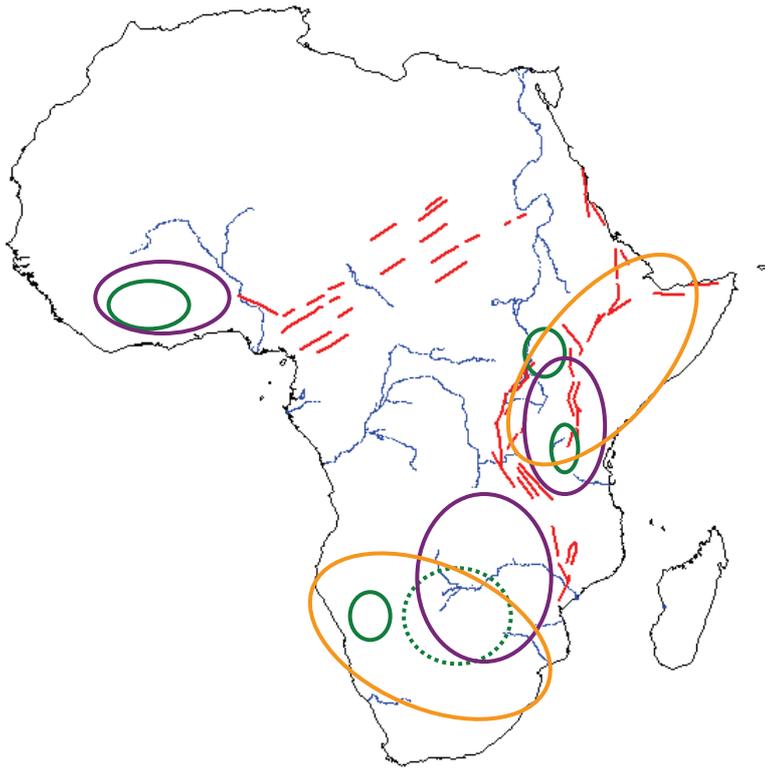


Figure 4. Delineating areas of genetic distinctiveness to advise the translocations of ungulates in Africa using existing phylogeographic data and surrogates for genetic distinctiveness. Purple circles- consistent areas of genetic distinctiveness based on molecular studies, orange circles- disjunct distributions of species and sister species, red lines- fault lines, blue lines- major rivers (of stream order 5 and above) and green circles- locations of hypothesised refugia (based on sampling sites in molecular studies; dashed lines- uncertainty).

DISCUSSION

Phylogeographic information is available for only 15.6 % of the 96 known African ungulate species, and most of these studies do not cover entire species ranges. In consequence, appropriate phylogeographic data to inform risk assessments for translocations is scarce. As has been mentioned Greig (1979) translocations raise concern for genetic introgression. Here different surrogates of genetic distinctiveness were investigated, as an alternative to the use of phylogeographic data for informing translocations, with the aim of providing information for evidence-based risk assessments of the likelihood of genetic introgression. Although the use of these surrogates requires a number of often controversial assumptions to be made (Table 1), in the absence of phylogeographic information, and the ongoing translocations being made for both economic and conservation reasons (Munthali & Mkanda, 2002; Matson *et al.*, 2004), little other option exists for informed decision-making. Below the utility of each of the proposed surrogates is discussed based on the results above, the validity of the assumptions made and opinions in the literature.

Phylogeographic structure

The assumption that molecular phylogeographic studies represent actual phylogeographic structuring in species is likely to depend on the extent of sampling and molecular markers used. For example, phylogeographic studies, undertaken by different authors on roan antelope, *Hippotragus equinus* (Matthee & Robinson, 1999; Alpers *et al.*, 2004) and sable antelope, *Hippotragus niger* (Matthee & Robinson, 1999; Pitra *et al.*, 2002) gave different results due to differences in the number of individuals sampled. Furthermore, it must be taken into account that molecular phylogeographic data does not indicate adaptive evolution, but only genetic structure due to long-term historical isolation (Gram & Sork, 1999; Reed & Frankham, 2001; Moritz, 2002).

The assumption based on the phylogeographic hypothesis (Avice *et al.*, 1987), that phylogeographic data can be extrapolated from one species to other species, has some limitations. First, extrapolation is only possible for geographical areas for which there is existing phylogeographic information (Avice, 1992). The central African region and country of South Africa generally remain devoid of phylogeographic data, preventing predictions for these areas based on existing information. Second, geographic ranges

should be of a similar size for extrapolation. Some species have small geographic ranges that show fine scale genetic patterns that are not comparable with the large ranges of species showing broad scale patterns. Lastly, concordance in phylogeography, at a landscape or biogeographic region scale, is reliant on species responding in the same way to zoogeographic barriers and climatic or geologically induced large-scale habitat shifts (Avice *et al.*, 1987; Riddle & Jones, 1996). Predicting the response of different species to such evolutionary processes could be based, in part, on habitat specialisation (Templeton & Georgiadis, 1996), but this will not necessarily be reliable.

Having highlighted the limitations and uncertainties of extrapolating phylogeographic data for African ungulates, information from other groups is considered to provide further insight into phylogeographic concordance between species. Support for concordance in phylogeographic patterns across different species and taxa has been divided. Some studies have found concordant phylogeographic patterns between different species and taxa (Avice 1992; Walker & Avice, 1998; marine animals- Dawson, 2001). Other studies have not found such evidence, but have concluded that the observed patterns were due to groups of species that had different life histories (e.g. birds- Zink, 1996), while other studies have found concordance in some regions but not in others (e.g. fishes- Bernatchez & Wilson, 1998; Taberlet, 1998).

Based on the information above, existing phylogeographic data will only be useful for designating population genetic structuring and advising translocations of those species and for those regions that are sufficiently sampled. For example, a prediction can be made that there will be structuring between southern and eastern Africa, a pattern of divergence that has often been attributed to the influence of the east African rift valley on habitat and species movement (Templeton & Georgiadis, 1995; Arctander *et al.*, 1999; Matthee & Robinson, 1999).

Subspecies

Subspecies designations have been a commonly used surrogate of population genetic structuring in animal species (Moritz, 2002), but have also been criticized due to the designation of subspecies being inconsistent and being based on few samples, limited geographical sampling, the variation of morphological traits between individuals and

lack of congruence between subspecies designations and genetic data (Mayr, 1982; Ryder, 1986; Avise *et al.*, 1987; Ball & Avise, 1992; Moritz, 2002; Zink, 2004). Subspecies designation in ungulates has largely been based on geographical location and morphological characters such as skull length, horn size, coat colour and coat patterning (e.g. Dorst & Dandelot, 1970; Meester & Setzer, 1971; East, 1999). Ungulate subspecies have been designated by different researchers at different times using different techniques, and for many species different subspecies are recognised by different authors (e.g. the subspecies designations in Wilson & Reeder (2005) differed from those in the phylogeographic studies in Table 2). However, there are also a large number of ungulate species without recognised subspecies. Due to inconsistencies in subspecies designations for ungulate species and the fact that congruence between subspecies and molecular phylogeographic data were only found for some species, subspecies are probably not a reliable surrogate for population genetic structuring, and therefore should not be used to assess the risk of translocations, unless no other data are available.

Ecoregions

When using ecoregions to assess phylogeographic data or predict phylogeographic patterns, several caveats should be borne in mind, including that ecoregions and biomes are often disjunct and that sampling sites need to be precise to assign individuals to the correct ecoregion, because ecoregions change over relatively short distances. There is limited data available at a scale appropriate to test the ecoregion concept for its applicability to African ungulate species. For example, for many existing phylogeographic studies few of the populations sampled were from the same ecoregion. The resolution of ecoregions disadvantages them when their performance is tested against other surrogates of a coarser resolution for which existing phylogeographic data matches more closely. However, Moodley & Bruford (2007) have thoroughly sampled the entire range of *Tragelaphus scriptus*, across sub-Saharan Africa. They found a strong relationship between haplogroups (although haplotypes can occur in multiple populations) and ecoregions, hypothesising that the species colonized, adapted to and persisted in ecoregions despite the different climate regimes of the Pleistocene. Based on the outcomes of their study, Moodley & Bruford (2007) suggest the use of biogeographical regions in the conservation of genetic diversity in African taxa more generally. However, extrapolation of the ecoregion concept from *T.*

scriptus to other ungulates would require that species responded in the same way to biogeographic processes as *T. scriptus*, an assumption that would be valid for a limited number of species. Furthermore, very few populations from the same ecoregions form monophyletic clades in *T. scriptus* and Moodley and Bruford (2007) needed to separate 6 of the biogeographic regions of Olson *et al.* (2001) to correspond with divisions of ecoregions by geomorphological barriers including the Gregory and East African rifts, because these barriers were responsible for monophyletic groupings of haplotypes within ecoregions. Other separations of ecoregions by Moodley and Bruford (2007) were ascribed to habitat discontinuity in ecoregions and distance between populations, but patterns of divergence also correspond to separation by the Niger and Nile rivers.

In the designation of genetically distinct populations for advising translocations the primary concern is maintaining irreplaceable evolutionary lineages that have evolved as a result of historical isolation (Moritz, 2002). Ecoregion designations are most likely to represent adaptive variation in species, which requires quantitative genetics and the analysis of phenotypes for its detection (Crandall *et al.*, 2000) and is not as important to conserve as it can be regenerated by recurrent selection (Moritz, 1999).

Evidence for the the importance of ecoregions in speciation comes from threespine sicklebacks, *Gasterosteus* species that have speciated in different habitats (Taylor & McPhail, 2000). Morphological divergence across different parapatric habitats has been found for forest vertebrates in Australia (Smith *et al.*, 2001) and a bird, the Little Greenbul, *Andropadus virens*, in central Africa (Smith *et al.*, 2005). Further support comes from the existence of contact zones between sister-species occurring between forest and savannah in Africa (Endler, 1982). However, divergence between forest and savanna, which has also been shown between populations of species such as elephants (Roca *et al.*, 2001) is divergence at a biome not ecoregion scale. Contact zones between sister-species occurring in different ecoregions have not been found for fauna of tropical Africa by Mayr & O'Hara (1986) or birds in South America (Cracraft *et al.*, 1988 and Prum, 1988 in Haffer, 1997).

The preliminary analysis done here suggests that ecoregions will not necessarily be a useful surrogate of genetic distinctiveness in ungulate species. However, the concept

holds considerable promise, as indicated by Moodley and Bruford (2007) and should be the focus of investigation in other exemplar taxa.

Disjunct distributions

Disjunct distributions between south-west and north-east Africa have been attributed by Coe & Skinner (1993) to the disjunct distribution of arid zones and the existence of the Brachystegia-Mopane woodland barrier. These disjunct distribution patterns have also been shown for carnivores (Coe & Skinner, 1993), ground squirrels (Herron *et al.*, 2005), plants (Jürgens, 1997) and ostrich (Freitag & Robinson, 1993). It is thought that south-western Africa became arid long before the rest of the continent and was the origin of many arid adapted lineages that later spread north and eastwards as vast areas of sub-Saharan Africa aridified (Pickford, 2004). This is supported by phylogeographic data for *Tragelaphus strepsiceros* that suggests the colonization of east Africa by populations from south-western Africa (Nersting & Arctander, 2001) and it has been predicted using climate modelling that, during the warm interglacial, tropical forest extended from coast to coast across central Africa separating more arid areas (Cowling *et al.*, 2008).

The concordance between the disjunct species distributions assessed here and the phylogeographic data correspond with the hypothesis of allopatric speciation (Mayr, 1942) that suggests that population genetic structuring is likely between isolated populations due to the absence of gene-flow. The importance of disjunct species distributions in population genetic structuring has been demonstrated for seabirds (Friesen *et al.*, 2007).

The disjunct distribution patterns that showed congruence are only applicable across two regions (south-west and north-east Africa) (Fig. 4) and therefore can only be used to predict population genetic structuring and advise translocations between these two regions. However, limited phylogeographic data for ungulates suggests that disjunct species distributions can be applied more widely to represent population genetic structure in those species with historically disjunct distributions. Thus, translocations between disjunct populations as defined here likely pose considerable introgression risks, and should not be undertaken.

Rivers

It has been suggested that rivers and faults play an important role in population genetic structuring of mammals (Grubb, 1999; Grubb *et al.*, 1999; Cotterill, 2003) and the separation of ungulate sister-species by rivers concurs with the main prediction of the riverine hypothesis. Based on the separation of sister-species by the well established Nile, Niger and Congo rivers these rivers are assumed to be important in the vicariance of ungulate species generally, but whether rivers that restrict the movement of some ungulate species, restrict the movement of all ungulate species is uncertain. The Niger and Congo drainage systems are thought to be more than 20 million years old and the Nile has been forming for 30 million years but stabilised *c.* 6 million years ago (Goudie, 2005) meaning that these rivers were established before the estimated times of divergence of most extant ungulate species (Hernández Fernández & Vrba, 2005). The Zambezi river is one of the largest rivers in Africa and its importance in vicariance has been proposed previously (Cotterill, 2003; Table 3), but it stabilised much more recently than the other three major African rivers (Nugent, 1990; Goudie, 2005; Stankiewicz & de Wit, 2005) likely making it less important in population genetic structuring in ungulates to date. The limited phylogeographic support for rivers in vicariance seen in Fig. 2 is due to little support for the Zambezi river having played a role in historically isolating populations. This is likely due to the age of this system and opportunity for circumnavigation by ungulate species. More relevant phylogeographic data are required to assess the importance of major African rivers in vicariance.

Outside of Africa, studies on the importance of rivers in vicariance have largely been conducted in Amazonia to test the riverine hypothesis, which was proposed for the Amazon river and its tributaries (Sick, 1967 and Capparella, 1988 in Haffer, 1997). Support for this drainage system as a source of vicariance has been varied but most consistent for the widest sections of the river. Some support for divergence caused by the Amazon drainage system has been found for birds (Aleixo, 2004; Hayes & Sewal, 2004), mammals (Peres *et al.*, 1996) amphibians (Funk *et al.*, 2007) and butterflies (Hall & Harvey, 2002) but other studies have found little support for the idea in mammals (Patton *et al.*, 1994) and amphibians (Gascon *et al.*, 1998).

The Congo, Niger and Nile rivers are most likely important in the vicariance of ungulate species. These rivers could act as surrogates for the delineation of genetic distinctiveness and could be useful to advise translocations of ungulates, but sufficient phylogeographic support for this hypothesis is lacking.

Faults

Based on the different sources of information used here, the east African rift valley appears to be a valuable surrogate for population genetic structuring. The east African rift valley is a barrier of considerable age that has restricted species movement in the past (Partridge *et al.*, 1995). It has been active for at least the past *c.* 30 million years (Partridge *et al.*, 1995; Burke, 1996) and the response of fauna to the rift system has largely been attributed to the heterogeneity of vegetation that is associated with its topographical complexity (Partridge *et al.*, 1995). The consideration of faults in the divergence of species is not new. The Alpine fault has been hypothesised as being a source of divergence in New Zealand based on disjunct species distributions (Heads, 1998) and the uplift of the Andes has been hypothesised as important in divergence of species in South America (Chapman, 1917; Croizat 1976 in Haffer, 1997; Emsley 1965). Indeed, support for this hypothesis has been found for primates (Cortes-Ortiz *et al.*, 2003), reptiles (Zamudio & Greene, 1997) and birds (Cracraft & Prum, 1988; Brumfield & Capparella, 1996; Eberhard & Bermingham, 2004, 2005; Cheviron *et al.*, 2005). For ungulates, mountains have proven a barrier to gene-flow in *Ovis dalli* (Worley *et al.*, 2004).

The evidence collated in this study suggests that the east African rift valley is a useful surrogate for delineating genetic distinctiveness and for advising translocations of ungulate species. Divergence may not necessarily be due to the rift valley physically restricting the movement of species, but rather to vegetational changes associated with the topography of the rift (Partridge *et al.*, 1995). Whether faults in other regions in Africa are responsible for vicariance would need to be tested with phylogeographic data. Nonetheless, movement of animals across the rift valley is contra-indicated.

Pleistocene refugia

Plio-Pleistocene climatic changes in Africa that caused shifts in habitats are thought to be particularly important in the evolution of African ungulates (Vrba, 1985;

deMenocal, 1995, 2004) and the forest refuge hypothesis is the most commonly accepted mechanism of diversification in the tropics (Mayr & O'Hara, 1986) with a number of refugia having been suggested for west and central Africa (Moreau, 1966; Kingdon, 1971, 1980; Hamilton, 1976; Grubb, 1982; Mayr & O'Hara, 1986; Hamilton, 1988; Maley, 1991; Prigogine, 1988 in Colyn *et al.*, 1991). Indeed, it has been suggested that duiker speciation has been driven by habitat fragmentation and its disruption of gene-flow (Jansen van Vuuren & Robinson, 2001). However, the Pleistocene refugia that have been hypothesised for ungulates in Africa (see Hewitt, 2004) have limited utility as a surrogate to designate genetic distinctiveness in ungulates as their actual locations and area of influence on genetic distinctiveness are unknown. Based on current knowledge, hypothesised Pleistocene refugia for ungulates are not particularly useful for advising translocations.

CONCLUSIONS

By using patterns in phylogeographic data and some of the proposed surrogates for delineating genetic distinctiveness in ungulate species, a few common regions of genetic distinctiveness have been identified (Fig. 4): the area south of the east African rift valley in southern Africa, the area east and north of the east African rift valley in east Africa and the area to the west of the Niger river in west Africa. Translocations between these regions are likely to be high risk and should be restricted. Based on current information, large faults, large rivers and disjunct distributions could be useful for advising translocations in the absence of phylogeographic data. However, more phylogeographic data are needed to substantiate this. A general rule that should be applied in considering translocations for supplementation or re-introduction is that individuals should be sourced from sites close to the site of release (Greig, 1979; Griffith *et al.*, 1989; Swart & Ferguson, 1997). Based on the broad scale of the information collated here, phylogeographic studies are recommended to advise translocations in species with small distribution ranges and species that occur outside the regions of Africa for which phylogeographic data are already available.

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- Chapter V -

Non-indigenous ungulates as a threat to biodiversity

INTRODUCTION

Non-indigenous species are a serious conservation problem (Wilcove *et al.*, 1998; Chapin *et al.*, 2000). They affect indigenous species from many different taxa by preying on them, changing their habitat, competing with them, hybridizing with them, and infecting them with pathogens or parasites (Mack *et al.*, 2000; Simberloff *et al.*, 2005). For example, bird extinctions have been caused by predation by mammals introduced to islands (Blackburn *et al.*, 2004), and introduced birds such as the Mallard duck, *Anas platyrhynchos*, have hybridised and introgressed with indigenous congeneric species (Rhymer *et al.*, 1994). Fish species extinctions have resulted from predation by introduced fish (e.g. Goldschmidt, 1996; but see Verschuren *et al.*, 2002) and introduced fish have hybridized and introgressed with indigenous fish (Echelle & Echelle, 1997; McDonald *et al.*, 2008). Introduced ants, such as the Argentine ant, *Linepithema humile*, have displaced several indigenous ant species worldwide (Human & Gordon, 1996; Holway, 1999) and the crazy ant, *Anoplolepis gracilipes*, has displaced a crab, *Gecarcoidea natalis*, causing ecosystem wide impacts (O'Dowd *et al.*, 2003). Indigenous plant species have been extirpated by the introduction of new diseases with introduced plants (e.g. Roane *et al.*, 1986), and displaced by introduced plants that provide poor habitat, use large amounts of water and alter fire regimes (e.g. Schmitz *et al.*, 1997). In consequence, introduced species cause substantial economic costs due to their impacts on agriculture, fisheries, forestry, biodiversity, ecosystem services and human health, and owing to the substantial costs of controlling them (Pimentel *et al.*, 2000; Simberloff *et al.*, 2005).

However, non-indigenous species also form the basis of substantial economic activity, which further promotes their introduction and public support, e.g. for agriculture (Diamond, 1998; Pimentel, 2002), aquaculture (Arndt *et al.*, 2002), the aquaria trade (Rixon *et al.*, 2005; Weigle *et al.*, 2005), horticulture (Reichard & White, 2001) and the pet trade (Cassey *et al.*, 2004; Brown, 2006). Therefore, the advantages and disadvantages of species introductions need rational assessment from a variety of perspectives. Indeed, the Convention on Biological Diversity (United Nations, 1993)

stipulates that risk assessment is required for actions (such as species introductions) that may cause harm to biodiversity.

Risk assessment involves the quantification of the probability of an undesirable outcome to an action (Burgman *et al.*, 1993), and it is fundamental in national policies regarding non-indigenous species introductions. National policies on non-indigenous species vary from using a strictly precautionary approach, involving the listing of permitted species (e.g. Australia (Anonymous, 1999)) to a strategy of listing prohibited species (e.g. United States (Anonymous, 1900), South Africa (Anonymous, 2004a), United Kingdom (Anonymous, 1932, 1976, 1981, 1996) and Japan (Anonymous, 2004b)) (see also Shine *et al.*, 2000; Takahashi, 2006). In countries that compile lists of prohibited species, species are categorised as invasive based on evidence that those species are a threat to human health or safety, the economy (e.g. fisheries, agriculture and forestry) or the environment including other species, habitats or ecosystems. In countries that use a list of prohibited species, proposals for the introduction of un-listed species require additional risk assessment of their potential impact (e.g. South Africa: Anonymous, 2004a).

For adequate risk assessment of vertebrate introductions, it is necessary to calculate informed estimates for the probabilities that a species will escape from private property, establish populations in the wild, negatively impact indigenous species, and the likelihood that it is able to be eradicated (Bomford, 2003; Andersen, 2008). Vertebrates are known to escape (Lever, 1985; Long, 2003) and they are likely to establish once introduced to an area (Forsyth & Duncan, 2001; Jeschke & Strayer, 2005). Once established, eradications will only be successful if the rate of removal exceeds the rate of population increase, immigration is prevented, all reproductive animals are removed, detection is possible at low densities, the benefits of eradication outweigh the costs, and there is a suitable socio-political environment (Bomford & O'Brien, 1995). However, the likelihood of introduced species having negative impacts on biodiversity is not always easy to predict.

Determining the likelihood that non-indigenous species will threaten biodiversity is important for risk assessment and also for the development and implementation of species-specific management policies (Hughey & Hickling, 2006). Stakeholders can

be unwilling to implement policies relating to non-indigenous species without evidence of their impacts (see Bradshaw *et al.*, 2007), but predictions of non-indigenous species impacts in a region or whether existing non-indigenous species in a region threaten biodiversity is often not documented in the scientific literature. However, it has been shown that invasiveness of a species in one place is a reasonable predictor of the likelihood of invasiveness elsewhere (Wittenberg & Cock, 2001; Rejmánek *et al.*, 2005). Therefore, if impacts of a non-indigenous species on biodiversity have been demonstrated somewhere in its introduced range, then it may be assumed that the species will impact biodiversity elsewhere in its introduced range.

Ungulates are a classic example of a group of animals that have been extensively translocated for economic reasons and as a result non-indigenous ungulates are widely distributed worldwide. Ungulates have been moved around for millennia, for food provision for humans (Diamond, 1998) and for sport hunting (Griffith, 1989; Forsyth & Duncan, 2001; Heinsohn, 2001), and based on their economic value they are highly valued by landowners (Demarais *et al.*, 1990; Castley *et al.*, 2001). However, for the same reasons as other taxa, concerns exist about the impact of non-indigenous ungulates on biodiversity (Demarais *et al.*, 1990; Castley *et al.*, 2001, Butler *et al.*, 2005; Bothma, 2005). Therefore, sound comprehension of the risks to biodiversity (and economic activities), of the introduction of non-indigenous ungulates is required to allow informed decisions to be taken, rational policy to be developed, and to convince landowners, where necessary, of the impact of non-indigenous ungulates on biodiversity. The first step in such an assessment is to determine the extent of the proposed risks. These risks can be assessed based on theory, on evidence from other taxa, and by quantifying evidence of the realised impacts of non-indigenous ungulates. Recently, the biodiversity impacts of a group of ungulates were assessed with mixed outcomes (Dolman & Wäber, 2008). Evidence was found for some categories of impact but not for others. Here I examine and quantify the evidence available in the literature for the impacts of non-indigenous ungulates on biodiversity with an aim to establish the extent of evidence that is available. The impacts examined are based on those impacts often cited for non-indigenous ungulates (see Demarais *et al.*, 1990; Castley *et al.*, 2001, Butler *et al.*, 2005; Bothma, 2005) and for non-indigenous species generally (White *et al.*, 2006).

METHODS

To obtain information on evidence of the impacts of non-indigenous ungulates (excluding domestic species that are not commonly hunted for sport) on biodiversity the literature was searched using ISI Web of Science (1987-2007) and Zoological Record (1864-2007). Generic and common names (see Box 1 in Chapter 3) were used with the following search terms ('introduce*', 'alien', 'extralimital', 'exotic', 'invasive' or 'feral') and ('abiotic', 'compete', 'competition', 'damage', 'disease', 'effect', 'erosion' 'facilitation', 'hybrid', 'impact', 'parasite', 'pathogen', 'predation' 'rooting', or 'vegetation'). The reference lists of the papers obtained during searches were browsed for any papers that might have been missed.

Evidence of the following impacts of non-indigenous ungulates on biodiversity was examined: 1. hybridization, 2. direct impacts on flora (herbivory, rooting, digging etc.), 3. predation, 4. direct impacts on abiotic processes (specifically soil system functioning), 5. exploitative competition impacting indigenous ungulates and other taxa, 6. apparent competition through predator-prey and parasite-host relationships impacting indigenous ungulates and other taxa, 7. facilitation and 8. trophic cascades.

Risks facing biodiversity from each type of impact were assessed using evidence from ungulates and by taking theory and evidence from other taxa into account. Impacts of non-indigenous ungulates on biodiversity, reported in studies, were assessed using the criteria in Table 1 to determine the certainty of the evidence that non-indigenous ungulates pose a threat to biodiversity. The criteria used to assess evidence were defined based on the methodology required to demonstrate population-level or ecosystem-level impacts. The strength of evidence for different non-indigenous ungulate species impacts in different countries was determined, and for each type of impact the number and proportion of cases with weak, moderate and strong evidence were calculated.

HYBRIDIZATION AND INTROGRESSION

Hybridization has seldom been demonstrated in the wild but it has been demonstrated extensively in captivity. Introgression in the wild has only been demonstrated conclusively for introduced sika deer, *Cervus nippon*, with indigenous red deer, *Cervus elaphus* (Goodman *et al.*, 1999).

Table 1. Criteria used to assess evidence for impacts of non-indigenous ungulates on biodiversity and the strength of that support.

Criteria, methodology and references	Strength of evidence
<p>Exploitative competition (Wiens, 1989; Law & Watkinson, 1989; Gurevitch <i>et al.</i>, 1992)</p> <p>C1 Two species use the same resource Food: observation, stomach analysis, faecal analysis, literature review, feeding morphology (worst); Habitat: observation, telemetry, habitat suitability modelling (worst)</p> <p>C2 The resource is limiting + C1</p> <p>C3 The indigenous species is negatively affected - population decline + C2</p> <p>C4 Direct relationship between population decline and extra species + C3</p> <p>Replicated field experiment (best), correlational</p>	<p>****</p> <p>****</p> <p>****</p> <p>****</p>
<p>Apparent competition (White <i>et al.</i>, 2006)</p> <p><i>Parasite/pathogen-host dynamics</i></p> <p>PH1 Non-indigenous species hosts parasite/pathogen of indigenous species</p> <p>PH2 Non-indigenous species is immune to parasite/pathogen + PH1</p> <p>PH3 Parasite/pathogen numbers are increased by presence of new host + PH2</p> <p>PH4 Parasite/pathogen causes a population decline in indigenous species + PH3</p> <p><i>Predator-prey dynamics</i></p> <p>PP1 Non-indigenous species provides a large prey base for predator</p> <p>PP2 Predator numbers are increased + PP1</p> <p>PP3 Predation on indigenous species is increased + PP2</p> <p>PP4 There is a decline in population numbers of indigenous species + PP3</p>	<p>****</p> <p>****</p> <p>****</p> <p>****</p> <p>****</p> <p>****</p> <p>****</p> <p>****</p>
<p>Hybridization (Rhymer & Simberloff, 1996)</p> <p>H1 Identification of hybrid Hybrid identified based on morphology Observed mating, pregnancy and birth in absence of any other mates Use of species specific haplotypes or allozymes</p> <p>H2 Hybrids fertile + H1 Observations of female hybrids with young Observations of female hybrids mating, pregnant and with young Karyotype analysis Histological analysis e.g. of semen and seminiferous tubules</p> <p>H3 Introgression has occurred + H2 Species specific haplotypes or allozymes</p>	<p>****</p> <p>****</p> <p>****</p> <p>****</p> <p>****</p> <p>****</p> <p>****</p> <p>****</p>
<p>Herbivory, rooting, digging and trampling</p> <p>H1 Indigenous plants are trampled, eaten or uprooted by non-indigenous ungulates</p> <p>H2 There is a reduction in the population numbers of indigenous plant species + H1</p> <p>Recovery studies with randomly stratified selection of replicated sites</p> <p>Correlational with randomly stratified selection of replicated sites</p> <p>Islands with and without introduced ungulates</p> <p>Exclosures with randomly stratified selection of replicated sites</p>	<p>****</p> <p>****</p> <p>****</p> <p>****</p>

Table 1. continued.

Criteria, methodology and references	Strength
Predation (by a few omnivorous ungulates)	
P1 Identification of species consumed Stomach analysis, faecal analysis, observation	****
P2 Decline in prey population numbers + P1 Correlational study with demographic investigation Exclosures with demographic investigation	****
P3 Direct relationship between predation and population decline + P2	****
Abiotic processes e.g. soil system functioning	
A1 Significant change in abiotic conditions Recovery studies with randomly stratified selection of replicated sites	****
Correlational with randomly stratified selection of replicated sites	****
Islands with and without introduced ungulates	****
Exclosures with randomly stratified selection of replicated sites	****
Facilitation (Schoener, 1993; White <i>et al.</i> , 2006)	
F1 Disturbance from non-indigenous species promotes indigenous species Correlational with randomly stratified selection of replicated sites	****
Islands with and without introduced ungulates	****
Exclosures/enclosures with randomly stratified selection of replicated sites	****
F2 Direct relationship demonstrated + F1	****
Trophic cascades (Strong, 1992; White <i>et al.</i> , 2006)	
TC1 Non-indigenous species provides large prey base for secondary predator	****
TC2 Secondary predator numbers are increased	****
TC3 Primary predator number are decreased	****
TC4 Indigenous prey species numbers are increased isotope ratios, observation and demographic studies	****

**** weak evidence, **** moderate evidence, **** strong evidence, **** very strong evidence

Hybridization between introduced blue wildebeest, *Connochaetes taurinus*, and indigenous black wildebeest, *C. gnou*, in the wild has been supported by anecdotal evidence of fertile hybrids (Fabricius *et al.*, 1988) and limited molecular data for introgression (Grobler *et al.*, 2005). However, of 544 potential inter-specific mate pairings between congeneric ungulate species, 61 congeneric hybridizations have been recorded in captivity of which 20 were known to result in fertile offspring (Table 2 in Appendix) based on observations of hybrid animals producing offspring. Forty hybridizations outside genera were also recorded, of which 7 hybridizations resulted in fertile offspring (Table 2 in Appendix). The current evidence for hybridisation and introgression in the field is insufficiently conclusive or extensive, but the topic has not been extensively researched. Hybridization between introduced and indigenous species is a topic that is generally under-researched despite introgression having already had a significant contribution towards the extinction of some species (Rhymer & Simberloff, 1996; Parker *et al.*, 1999; Allendorf *et al.*, 2001). Considering introgression theory and examples from other taxa, the introduction of congeneric

species that are likely to hybridize with indigenous species and produce fertile offspring poses a major risk for ungulate introductions. However, field evidence for the realization of such risks is minimal.

HERBIVORY, ROOTING AND DIGGING

Strong evidence for the impacts of introduced ungulates on vegetation structure and composition has been obtained from exclosure studies for 55% of ungulate species introduced to different countries, moderate evidence has been obtained from correlative studies, the recovery of indigenous flora following non-indigenous ungulate eradication and islands with and islands without ungulates and weak evidence has been obtained by observations for 15 % of ungulate species introduced to different countries (Table 2). Overall the studies collated here suggest that non-indigenous ungulates have had substantial impacts on vegetation structure and composition in systems with and without indigenous ungulates (Table 2). Herbivory by non-indigenous species is commonly known to have substantial impacts on flora, particularly on islands, where introduced herbivores can cause plant extinctions (Courchamp *et al.*, 2003). Based on the collated evidence the introduction of non-indigenous ungulates should be considered a substantial risk to flora especially in confined areas, such as islands.

Table 2. Impacts of non-indigenous ungulates on flora.

Introduced species and methodology	Place and evidence	References	Strength of evidence
<i>Bos javanicus</i> Correlational	AUSTRALIA: change in cover, abundance and composition of plants and reduced recruitment	Bowman & Panton, 1991	****
<i>Bubalus bubalis</i> Correlational Exclosure Removal and recovery	AUSTRALIA: change in plant composition, reduced canopy height, reduced ground level biomass and litter; change in competitive relationships and fire fuel load, reduced tree growth and change in tree demography	Braithwaite <i>et al.</i> , 1984; Minchin & Dunlop, 1989; Skeat <i>et al.</i> , 1996; Werner, 2005; Werner <i>et al.</i> , 2006; Petty <i>et al.</i> , 2007	****
<i>Cervus elaphus</i> Correlational Exclosure	ARGENTINA: change in rejuvenation and plant composition CHILE: change in recruitment and plant composition	Veblen <i>et al.</i> , 1989; 1992 Ramírez <i>et al.</i> , 1981	****
Exclosure	NEW ZEALAND: reduced tree recruitment and growth, reduced abundance, reduced structure and composition of species, change in litter quality	Allen <i>et al.</i> , 1984; Wardle, 1984; Smale & Kimberley, 1994; Nugent <i>et al.</i> , 1997; Wardle <i>et al.</i> , 2001*; Forsyth <i>et al.</i> , 2002; Husheer <i>et al.</i> , 2003, 2005; Husheer, 2007	****
Observation	Secretary Island, NEW ZEALAND: reduced plant abundance	Mark & Baylis, 1975	****

Table 2. continued.

Introduced species and methodology	Place and evidence	References	Strength of evidence
<i>Cervus nippon</i> Islands with and without Exclosure Exclosure Correlational	Queen Charlotte Islands, BRITISH COLOMBIA: change in plant community structure	Gaston <i>et al.</i> , 2006	****
	ENGLAND: change in plant community structure and composition	Diaz <i>et al.</i> , 2005	****
	IRELAND: reduced tree recruitment	Perrin <i>et al.</i> , 2006	****
	NEW ZEALAND: reduced tree recruitment	Davidson & Fraser, 1991; Allen & Allan, 1997; Husheer <i>et al.</i> , 2006	****
<i>Dama dama</i>	NEW ZEALAND: change in succession pathway	Smale <i>et al.</i> , 1995	****
<i>Giraffa camelopardalis</i> Correlational, exclosure	South Africa (extralimital): change in tree composition	Bond & Loffell, 2001	****
<i>Muntiacus reevesi</i> Exclosure	ENGLAND: change in plant composition, reduced recruitment and change in abundance of species	Cooke & Farrell, 2001	****
<i>Odocoileus virginianus</i> Exclosure, Removal and recovery	Stewart Island, NEW ZEALAND: reduced tree recruitment	Stewart & Burrows, 1989	****
<i>Odocoileus virginianus</i> Islands with and without Correlational	Anticosti Island, CANADA: reduced lichen, increased sedges and grasses, change in composition of plants, reduced growth and recruitment, reduced tree species	Chouinard & Filion, 2001, 2005; Potvin <i>et al.</i> , 2003; Pellerin <i>et al.</i> , 2006	****
<i>Oreamnos americanus</i>	UNITED STATES: change in plant composition	Scheffer, 1993	****
<i>Rangifer tarandus</i> Exclosure	South Georgia Island: change in plant composition and cover	Vogel <i>et al.</i> , 1984; Leader-Williams <i>et al.</i> , 1987	****
<i>Rupicapra rupicapra</i>	CZECH REPUBLIC: change in plant structure	Homolka & Heroldová, 2001	
<i>Rusa timorensis</i>	AUSTRALIA: reduced plant recruitment and growth	Keith & Pellow, 2005	
<i>Sus scrofa</i> Correlational	AUSTRALIA: rooting and digging leads to reduced seedling numbers, reduced survival and reduced plant species richness	Alexiou, 1983; Hone, 1988, 2002; Bowman & McDonough, 1991; Bowman & Panton, 1991; Mitchell <i>et al.</i> , 2007	****
	NEW ZEALAND: reduced plant recruitment	Challies, 1975	****
	Auckland Island, NEW ZEALAND: reduced plant abundance	Singer <i>et al.</i> , 1984; Kotanen, 1995; Cushman <i>et al.</i> , 2004	****
	UNITED STATES: Disturbance leads to reduced ground vegetation cover and reduced leaf litter; increased exotic plants, change in plant species composition, reduced plant species richness		
	Hawaai, USA: reduced plant recruitment	Sweetapple & Nugent, 2004	****

* not only *Cervus elaphus*; **** weak evidence, *** moderate evidence, ** strong evidence

PREDATION BY OMNIVOROUS UNGULATES

Several studies have assessed the stomach contents of culled *Sus scrofa* in their introduced range and these studies report various animal species that have been consumed (Table 3). Only a small group of ungulates are omnivorous and the evidence for ungulates posing a problem for biodiversity through predation is generally weak. Animal matter typically only forms a small proportion of the diet of *Sus scrofa* and there is little conclusive evidence that predation has led to significant population declines of indigenous species. For example, Fordham *et al.* (2007) found that a turtle, *Chelodina rugosa*, compensated for predation from *S. scrofa* by increasing recruitment.

Table 3. Records of predation by *Sus scrofa* in its introduced range and the strength of evidence that predation led to population declines in indigenous species.

Prey	Reference	Strength of evidence
Birds e.g. <i>Laterallus spilonotus</i> , <i>Megadyptes antipodes</i> , <i>Pachyptila desolata</i> , <i>Pterodroma</i> <i>phaeopygia</i> , <i>Puffinus huttoni</i> , <i>Tricholimnas sylvestris</i>	Harris, 1970; Challies, 1975; Wood & Roak, 1980; Harper, 1983; Miller & Mullette 1985; Coblenz & Baber, 1987; Howell & Webb, 1990; Holden, 1994; Cuthbert, 2002; Gibbs <i>et al.</i> , 2003	****
Reptiles e.g. <i>Chelonia mydas</i> , <i>Chelodina rugosa</i> , <i>Conolophus</i> subcristatus, <i>Geochelone</i> <i>elephantopus</i> , <i>Dromicus dorsalis</i> , <i>Tropidurus jacobii</i>	MacFarland <i>et al.</i> , 1974; Wood & Roak, 1980; Coblenz & Baber, 1987; Fordham <i>et al.</i> , 2006	****
Oligochaetes	Henry & Conley, 1972; Challies, 1975; Wood & Roak, 1980; Coblenz & Baber, 1987; Thomson & Challies, 1988; Chimera <i>et al.</i> , 1995	****
Gastropods	McIlroy, 2001	****
Coleoptera, Hymenoptera, Lepidoptera, Orthoptera	Coblenz & Baber, 1987	****
Amphipods	Challies, 1975	****

**** weak evidence, *** moderate evidence, ** strong evidence

In Texas, predation on animals is thought to be less concerning than other impacts caused by *Sus scrofa* (Taylor & Hellgren, 1997), but in other areas, such as on islands, where food may be limited or endangered species may be vulnerable, predation by *S. scrofa* could be problematic. Introduced predatory species are responsible for a large number of extinctions (Sinclair *et al.*, 1997; Goldschmidt, 1996; Blackburn *et al.*,

2004) and other non-indigenous omnivorous species such as rats have caused extinctions on islands (Courchamp *et al.*, 2003). Therefore predation by *Sus scrofa* should not be discounted as a risk on islands.

IMPACTS ON SOIL SYSTEM FUNCTIONING

Little evidence was found that non-indigenous ungulates impact on soil system functioning. As expected, increases in soil erosion have been shown (e.g. Scheffer, 1993; Sierra, 2001) and the tilling of soil by *Sus scrofa* has caused plant death (Kotanen, 1995). Singer *et al.* (1984) found that *Sus scrofa* is responsible for mixing soil horizons, increasing water nitrogen, increasing soil nitrogen, reducing leaf litter and increasing the leaching of minerals from leaf litter and soil. The impacts that have been associated with changes in soil properties caused by *Sus scrofa* include the displacement of small mammals (Singer *et al.*, 1984) and the reduction of the density and number of collembola species (Vtorov, 1993) and micro-arthropods (Wardle *et al.*, 2001). Despite the paucity of evidence of impacts on soil system functioning, it is a concern for non-indigenous ungulates other than *Sus scrofa*. Non-indigenous species are generally known to impact soil system functioning by altering processes such as nutrient cycling (Chapin *et al.*, 2000; Dukes & Mooney, 2004) and non-indigenous ungulates should be no exception, as ungulates play an important role in nitrogen cycling (Hobbs, 1996). Therefore, non-indigenous ungulates pose a risk to the alteration of soil system functioning.

EXPLOITATIVE COMPETITION

The evidence for competition between non-indigenous and indigenous ungulates is weak as very few studies sufficiently satisfy the conditions required to demonstrate competition (see Table 1), and replicated experimental work is lacking (Table 4). Only 17.4 % of non-indigenous species impacts from competitive exclusion in different countries were supported by strong evidence. Two studies show good evidence of competition between non-indigenous ungulates and other taxa leading to substantial population declines of indigenous species on islands e.g. introduced white-tailed deer, *Odocoileus virginianus*, and an indigenous bear, *Ursus americanus* (Côté, 2005) and introduced sika deer, *Cervus nippon*, and indigenous invertebrates (Allombert *et al.*, 2005). A study with some of the strongest evidence for competition between introduced and indigenous ungulates used enclosure experiments in Texas

which showed population declines in indigenous ungulate species (Harmel, 1978), but the replication in these experiments was insufficient. Field experiments are most useful for demonstrating competition but have been conducted in few instances. Most studies only report habitat overlap, dietary overlap and dietary capacity as lines of evidence that competition could be occurring between introduced and indigenous ungulates and very few studies show that resources are limited or that populations have declined (Table 4).

Table 4. The evidence used to support exploitative competition of non-indigenous ungulates with indigenous species. 1. Habitat overlap (HO) or habitat preference (HP), 2. Dietary overlap (DO) or broader diet (BD), 3. Limited resources available (LR), 4. Demonstrated population decline (PD) and 5. Direct relationship demonstrated (DR).

Introduced species	Indigenous species	Place, evidence and methodology	References	Strength of evidence
<i>Ammotragus lervia</i>	<i>Capra pyrenaica</i>	HP DO LR PD DR Habitat suitability modelling, Spain	Acevedo <i>et al.</i> , 2007	****
<i>Ammotragus lervia</i>	<i>Odocoileus virginianus</i>	HO DO LR PD DR Enclosure, Texas, USA	Butts <i>et al.</i> , 1982	****
<i>Ammotragus lervia</i>	<i>Odocoileus hemionus</i>	HO DO LR PD DR Field study, Texas & New Mexico, USA	Bird & Upham, 1980; Krysl <i>et al.</i> , 1980; Simpson & Gray, 1983	****
<i>Antilope cervicapra</i>	<i>Odocoileus virginianus</i>	HO BD LR PD DR Enclosure, Texas, USA	Butts <i>et al.</i> , 1982; Henke <i>et al.</i> , 1988	****
<i>Axis axis</i>	<i>Odocoileus virginianus</i>	HO DO LR PD DR Enclosure, Texas, USA	Harmel, 1978; Butts <i>et al.</i> , 1982; Baccus <i>et al.</i> , 1985; Henke <i>et al.</i> , 1988	****
<i>Cervus elaphus</i>	<i>Hippocamelus bisculus</i>	HO DO LR PD DR Faecal analysis, Argentina	Galende <i>et al.</i> , 2005	****
<i>Cervus elaphus</i>	<i>Lama glama</i>	HO DO LR PD DR Faecal analysis, Argentina	Bahamonde <i>et al.</i> , 1986; Flueck, 1996	****
<i>Cervus elaphus</i>	<i>Odocoileus hemionus</i>	HO DO LR PD DR Faecal analysis, Alaska	Kirchhoff & Larsen, 1998	****
<i>Cervus elaphus</i>	<i>Callaenas cinera</i>	HO DO LR PD DR Literature review, New Zealand	Leathwick <i>et al.</i> , 1983	****
<i>Cervus elaphus</i>	<i>Porphyrio hochstetteri</i>	HO DO LR PD DR Field study, New Zealand	Mills & Mark, 1977; Lee & Jamieson, 2001	****
<i>Cervus nippon</i>	<i>Odocoileus virginianus</i>	HO DO LR PD DR Enclosure & faecal analysis, Texas, USA	Butts <i>et al.</i> , 1982; Baccus <i>et al.</i> , 1985; Keiper, 1985	****
<i>Cervus nippon</i>	Invertebrates	HO DO LR PD DR Field study, Haida Gwaii, Canada	Allombert <i>et al.</i> , 2005	****

Table 4. continued.

Introduced species	Indigenous species	Place, evidence and methodology	References	Strength of evidence
<i>Dama dama</i>	<i>Odocoileus virginianus</i>	HO DO LR PD DR Enclosure, Texas, USA	Butts <i>et al.</i> , 1982; Baccus <i>et al.</i> , 1985; Feldhamer & Armstrong, 1993	*****
<i>Muntiacus reevesi</i>	<i>Capreolus capreolus</i>	HO DO LR PD DR Field study, England	Hemami <i>et al.</i> , 2004; 2005	*****
<i>Odocoileus virginianus</i>	<i>Ursus americanus</i>	HO DO LR PD DR Field study, Anticosti island, Canada	Côté, 2005	*****
<i>Oryx gazella</i>	<i>Odocoileus hemionus</i>	HO BD LR PD DR Anecdotal, New Mexico, USA	Smith <i>et al.</i> , 1998; Bender <i>et al.</i> , 2003	*****
<i>Oryx gazella</i>	<i>Ovis canadensis</i>	HO BD LR PD DR Anecdotal, New Mexico, USA	Smith <i>et al.</i> , 1998; Bender <i>et al.</i> , 2003	*****
<i>Ovis aries</i>	<i>Capreolus capreolus</i>	HO DO LR PD DR Faecal analysis, Czech Republic	Heroldová, 1996	*****
<i>Rupicapra rupicapra</i>	<i>Cervus elaphus</i>	HO DO LR PD DR Faecal & rumen analysis, Czech Republic	Homolka & Heroldová, 2001	*****
<i>Sus scrofa</i>	<i>Pecari tajacu</i>	HO DO LR PD DR Field study, Texas, USA reduced population densities, habitat partitioning, <i>S. scrofa</i> better exploiter	Ilse & Hellgren, 1995; Gabor & Hellgren, 2000; Gabor <i>et al.</i> , 2001; Sicuro <i>et al.</i> , 2002	*****
<i>Sus scrofa</i>	<i>Tayassu pecari</i>	morphology indicates larger dietary capacity	Sicuro <i>et al.</i> , 2002	*****
<i>Rangifer tarandus</i>	<i>Hydromedion sparsutum</i>	HO DO LR PD DR Feeding trial, South Georgia	Chown & Block, 1997	*****
<i>Tragelaphus angasii</i>	<i>Tragelaphus scriptus</i>	HO DO LR PD DR Anecdotal, South Africa.	Coates & Downs, 2005	*****

***** weak evidence, **** moderate evidence, *** strong evidence

Competition theory suggests that if two species are using the same resource and that resource is limiting, the competitively inferior species will experience a population decline (Mac Nally, 1983; Arthur, 1987; Law & Watkinson, 1989; Wiens, 1989). However, Davis (2003) highlights the lack of evidence for non-indigenous species causing extinctions of indigenous species through competition for resources, suggesting that competition from non-indigenous species is not a significant threat to biodiversity. Indeed, Gurevitch *et al.* (1992) found that for indigenous herbivorous species, intraspecific competition is more important than interspecific competition. However, there is substantial evidence for competitive exclusion by non-indigenous species e.g. the fire ant, *Solenopsis invicta* and the Argentine ant, *Linepithema humile* (Mooney & Cleland, 2001) competitively exclude indigenous ant species, and non-indigenous insects and arachnids competitively displace indigenous species more

often than indigenous species displace each other (Reitz & Trumble, 2002). Islands, especially, have been arenas of extinctions of indigenous species due to competitive exclusion by introduced species (Brown, 1989; Diamond, 1984) and during the Great American interchange the intercontinental mixing of faunas is thought to have resulted in North American marsupial carnivores replacing South American ones by competitive exclusion (Webb, 1991, Vermeij, 1991). Competition theory and evidence from ungulates and other taxa suggest that there is a risk that non-indigenous ungulates could displace indigenous species by exploitative competition and lead to extirpations, especially in small, closed, resource-limited systems such as islands. However, convincing field data are often lacking.

APPARENT COMPETITION

Little evidence was found for apparent competition. Only one study (Roemer *et al.*, 2001) provides evidence for hyper-predation (Table 5). Roemer *et al.* (2001) used demographic information, observations and modelling to give strong evidence for hyper-predation induced by *Sus scrofa* leading to population declines in an indigenous species (Table 5). However, weaker evidence is available for parasites as mediators of competition between introduced and indigenous ungulates. Two studies use circumstantial evidence to infer the transfer of non-indigenous parasites by non-indigenous ungulates to indigenous ungulate species and these studies don't demonstrate population declines in the indigenous species (Table 5). Other studies concerning parasites and pathogens of non-indigenous ungulate species fail to demonstrate a link between the pathogens and parasites of introduced and indigenous ungulates, they fail to prove the transfer of a novel parasite or pathogen to an indigenous species and they fail to prove increased pathogen or parasite numbers as the consequence of a novel ungulate host. Such investigations would require sufficient data on parasite/pathogen-host dynamics, including parasite/pathogen species composition and population demographics, before and after ungulate introductions, but such data are lacking. Instead, studies investigate pathogens and parasites of sympatric non-indigenous and indigenous ungulate species (e.g. Leader-Williams, 1980; Davidson & Crow, 1983; Davidson *et al.*, 1985, 1987), studies investigate parasites (e.g. Dzieciolowski & Clarke, 1990; Fourie *et al.*, 1991) and pathogens (Bender *et al.*, 2003) in introduced ungulates and some studies show that the translocation of ungulates can result in the introduction of novel parasites such as

ticks to new areas (Braack *et al.*, 1995; Bram & George, 2000). In most cases the non-indigenous ungulates that were studied were well established and investigations often found that they had lower parasite burdens, were not susceptible to the parasites of indigenous ungulates and had better body condition than sympatric indigenous species, which was attributed to a larger dietary capacity (e.g. Davidson & Crow, 1983; Davidson *et al.*, 1987).

Despite the lack of evidence for apparent competition in non-indigenous ungulates, theory and evidence from other taxa suggest that it is a concern. Theory suggests that apparent competition will occur if non-indigenous species cause increased numbers of predators, parasites or pathogens to which indigenous species are more susceptible (Holt, 1977; Holt & Lawton, 1994; Daszak *et al.*, 2000; Prenter *et al.*, 2004; Woolhouse *et al.*, 2005; White *et al.*, 2006). For example, moose, *Alces alces*, can be competitively excluded by white-tailed deer, *Odocoileus virginianus*, which hosts meningeal worms, *Paralaphostogylus tenuis*, that can be fatal to *A. alces* (Schmitz & Nudds, 1994), the gray squirrel, *Sciurus carolinensis* competitively excludes the red squirrel, *Sciurus vulgaris*, by infecting it with parapoxvirus (Tompkins *et al.*, 2003; Rushton *et al.*, 2006) and rinderpest introduced by cattle, translocated from Asia, caused substantial population declines in African ungulates (Mack, 1970; Plowright, 1982). The rinderpest example in particular highlights the risk of apparent competition from non-indigenous ungulates and suggests that apparent competition requires consideration despite the limited evidence available. Whether non-indigenous ungulates are responsible for hyper-predation more widely requires more field data.

FACILITATION

Few studies have demonstrated facilitation by introduced ungulates, but five of the six studies that were found provided strong evidence (Table 5). In all instances, non-palatable (often non-indigenous) plant species were facilitated due to introduced ungulate species selectively feeding on palatable species. The same is true for herbivores generally; non-indigenous herbivores facilitate non-indigenous plants by reducing indigenous plant abundance (Parker *et al.*, 2006). The facilitation of non-indigenous species by other non-indigenous species is recognised as a substantial problem and includes the dispersal of non-indigenous plants by non-indigenous

animals and facilitation due to habitat modification induced by non-indigenous species (Simberloff & Von Holle, 1999).

Table 5. Indirect impacts on biota caused by introduced ungulates (excluding exploitative competition).

Type of impact	Introduced species and place	Mediator	Affected species	References	Strength of evidence
Apparent Competition	<i>Antidorcas marsupialis</i> SOUTH AFRICA	<i>Bronchonema magna</i> (parasite)	<i>Damaliscus pygargus</i>	Meltzer <i>et al.</i> , 1993	***
Apparent Competition	<i>Dama dama</i> UNITED STATES	<i>Bovicola tibialis</i> (parasite)	<i>Odocoileus hemionus</i>	Westrom <i>et al.</i> , 1976	***
Apparent Competition	<i>Sus scrofa</i> Channel islands, UNITED STATES	<i>Aquila chrysaetos</i> (predator)	<i>Urocyon littoralis</i>	Roemer <i>et al.</i> , 2001	***
Facilitation	<i>Bubalus bubalis</i> AUSTRALIA	increase in disturbance; decrease in indigenous plants	increase in exotic plants (<i>Mimosa pigra</i>)	Cowie & Werner, 1993; Lonsdale, 1993	***
Facilitation	<i>Cervus nippon</i> IRELAND	increase in bryophytes	increase in <i>Rhododendron ponticum</i>	Cross, 1981	***
Facilitation	<i>Cervus nippon</i> ENGLAND	increase in <i>Spartina anglica</i>	increase in <i>Hydrobia ulvae</i> , <i>Gammarus sp.</i> , <i>Nereis diversicolor</i>	Diaz <i>et al.</i> , 2005	***
Facilitation	<i>Muntiacus reevesi</i> ENGLAND	increase in grasses and sedges (avoided)	increase in lepidopteran spp.	Cooke & Farrell, 2001	***
Facilitation	<i>Rangifer tarandus</i> South Georgia	decrease in <i>Parodiocloa flabellate</i> & <i>Acaena magellanica</i>	increase in <i>Poa annua</i>	Leader-Williams, 1989	***
Trophic cascade	<i>Sus scrofa</i> Channel islands, UNITED STATES	increase in <i>Aquila chrysaetos</i>	increase in <i>Spilogale gracilis</i>	Roemer <i>et al.</i> , 2002	***

*** weak evidence, ** moderate evidence, * strong evidence

Due to the large number of ungulates that feed selectively, influence nitrogen cycling and modify habitats (see above) the facilitation of non-indigenous plant species is likely to be a common risk associated with non-indigenous ungulates.

TROPHIC CASCADES

Evidence exists for only one species, *Sus scrofa*, causing a trophic cascade and this was on the Channel Islands (Roemer *et al.*, 2002). *Sus scrofa* is the only omnivorous commonly-introduced ungulate species but trophic cascades have not been demonstrated for this species in the role of a secondary predator. *Sus scrofa* provides an abundant food source for a secondary predator and the increase of this predator indirectly benefits the prey of the primary predator species in the system (Table 5, Roemer *et al.*, 2002). For other non-indigenous taxa, trophic cascades have mostly been shown to cause ecosystem level impacts in aquatic systems but could be as important in terrestrial systems (White *et al.*, 2006). Further studies are needed to investigate the role of non-indigenous ungulates in increasing secondary predator numbers and causing trophic cascades.

CONCLUSIONS

Categorising the different impacts that non-indigenous ungulates have on biodiversity by level of threat is useful for risk assessment. The greatest threat is likely posed by non-indigenous species that perform a novel function at the site of introduction, such as an introduced predator on an island devoid of natural predators or an introduced nitrogen-fixing tree in an area with nitrogen poor soil (Simberloff, 1991; Ruesink *et al.*, 1995). Non-indigenous ungulates perform novel functions in systems devoid of indigenous large herbivores through herbivory and increasing soil nitrogen (Singer *et al.*, 1984). Species that alter disturbance regimes such as erosion and fire regimes also have large impacts (Mack & D'Antonio, 1998) and non-indigenous ungulates have been shown to do both. Non-indigenous ungulate impacts could be assessed based on the likelihood they will cause extinctions of indigenous species. If the extinction of indigenous species is considered at different scales (local displacement or extirpation to global extinction (see Carlton *et al.*, 1999)), then the different categories of impact can be placed on a continuum from impacts causing population declines, population displacement and local extinctions, to regional and global extinctions.

Herbivory on islands or in areas with endemic flora can cause global extinctions of plant species (Vitousek, 1988; Atkinson, 1989; Courchamp *et al.*, 2003). Competition can result in local displacement and extirpation (Côté, 2005), but is likely to result in fewer extinctions than herbivory (see Davis, 2003; Gurevitch & Padilla, 2004).

Hybridization could lead to extinction of ungulate populations if the population of the indigenous species is small, reproductive barriers are not sufficient, the hybrid offspring are fertile, or show hybrid vigour and the population growth rate of the non-indigenous species and hybrids are higher than that of the indigenous species (Wolf *et al.*, 2001). As yet hybridization has not resulted in extinction of an indigenous ungulate species. Global analyses of extinction threats from non-indigenous species show hybridization is a lesser threat than competition, herbivory or predation (Gurevitch & Padilla, 2004). Analyses by Gurevitch & Padilla (2004) also show that for the United States feral pigs are an extinction threat to more species than competition, predation, herbivory and hybridization from other non-indigenous species (excluding feral and domestic animals). Disease introduction by non-indigenous ungulates could result in population declines and extinctions, but this is less likely to occur than extinctions from predation, herbivory and competition (see Gurevitch & Padilla, 2004). However, for all of the different impacts from non-indigenous ungulates, mentioned above, more evidence is required. Despite the substantial concerns for impacts of non-indigenous ungulates on biodiversity that are often mentioned in the literature, this study demonstrates that the evidence available for these impacts is far from comprehensive. Future investigations should aim to satisfy the criteria necessary to sufficiently demonstrate the impacts of non-indigenous ungulates on biodiversity. It is suggested that to demonstrate the impacts of non-indigenous ungulates exclosure and enclosure experiments should be used and population declines in indigenous species should be shown.

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- Chapter VI -

Conclusions

Ungulate translocation management in South Africa

This thesis has been concerned exclusively with the evidence for impacts of ungulate translocations. It has examined biotic homogenization, introduction pathways, the potential and realized impacts of translocations, and the extent to which surrogate measures may be used to determine whether translocations among populations are likely to result in introgression. In consequence, it provides considerable information that can be used for the further development of management policies for ungulate translocation in South Africa. To this end, the conclusions are presented here in the form of an *Information Paper* of the kind typically put forward at meetings of international conventions.

SUMMARY

1. Ungulate translocations and introductions have been extensive in South Africa (Chapters 2 & 3) but little is known of the impacts of these translocations (Chapters 3). Although policy exists to limit translocations, even if it were implemented the numbers and extent of extralimital and extraregional ungulates already introduced are great and it is most likely these animals will establish and spread if they have not already done so (Forsyth *et al.*, 2001; Jeschke & Strayer, 2005). This information paper highlights what is known about the extent and impacts of ungulate translocations in South Africa and makes recommendations for the future management and research of ungulate translocations and introductions in South Africa.

INTRODUCTION

2. Introductions and translocations of ungulate species in South Africa are substantial (Chapters 2 & 3) and have led to the homogenization of ungulate biotas (Chapter 2) and extensive range changes of indigenous ungulate species (Chapter 3).
3. Non-indigenous ungulate species, both extralimital (species translocated outside their 'historical' distribution ranges) and extraregional (species from outside a geopolitical

region, in this case South Africa) are economically important to the hunting and tourism industries in South Africa (Castley *et al.*, 2001; Lindsey *et al.*, 2006).

4. Based on the ecology of invasive species (Williamson *et al.*, 1996; Mack *et al.*, 2000) and literature specifically documenting the impacts of non-indigenous ungulates on biodiversity (Dolman & Wäber, 2008; Chapter 5) it is expected that non-indigenous ungulates will be harmful to biodiversity in South Africa. Non-indigenous ungulates are known to alter habitat (Wardle *et al.*, 2001), compete with (Baccus *et al.*, 1985; Côté, 2005), eat (Fordham *et al.*, 2006), infect (Meltzer, 1993) and hybridize with (Goodman *et al.*, 1999) indigenous species.
5. However, little evidence of the impacts of extralimital and extraregional ungulates is available for South Africa (Chapter 3) and is much needed for convincing landowners of the threat that non-indigenous ungulates pose to biodiversity, for informing policy and prioritizing management action.
6. South Africa's Biodiversity Act (Anonymous, 2004) and its supporting documents (Anonymous, 2007) restrict the introduction and translocation of species, including the translocation of ungulate species within their 'historical' distribution ranges between 'population ranges' (Anonymous, 2007).
7. The listing of extraregional ungulate species and the designation of 'population ranges' has been based on limited information on the impacts of non-indigenous ungulates on biodiversity in South Africa and limited molecular work on indigenous ungulates in South Africa.
8. Based on the extent of ungulate translocations in South Africa to date (Chapter 3) and limited resources available for enforcing national policies throughout the country, it seems unlikely that the much-needed regulations will be comply with, and even if they are, many extralimital and extraregional ungulates are already distributed throughout the country (Chapter 3).
9. This information paper aims to collate information regarding ungulate translocations of three types in South Africa: extraregional introductions, extralimital introductions and indigenous species translocations. Ungulates here refers to the orders Artiodactyla and Perissodactyla (following Wilson and Reeder, 2005), primarily because these species are important to the game and hunting industries responsible for the majority of introductions. Information about policy, extent, drivers, pathways and impacts of ungulate translocations in South Africa is outlined as well as recommendations for future research and management of these translocations are made.

EXTRAREGIONAL INTRODUCTIONS

10. **Policy:** The National Environmental Management: Biodiversity Act (NEMBA) (Anonymous, 2004) restricts the movement of extraregional species (except those exempted by the Minister) without a permit, and the granting of a permit requires a risk assessment (Anonymous, 2004). The Act also states that persons responsible for the introduction of an extraregional ungulate can be held liable if it spreads and causes harm to biodiversity, and that the onus is on them to finance the control and/or removal of the species if it is required (Anonymous, 2004).
11. **Extent:** Globally, South Africa is second to the U.S.A. for the number of ungulate species that have been introduced to any country (Chapter 3). Extraregional introductions in South Africa have significantly increased since the inception of commercial hunting in the 1960s. Since 1965, 18 wild extraregional ungulate species have been advertised in *Landbou Weekblad* in 158 quarter-degree grid-cells (QDGCs) in South Africa (Chapter 3) and based on the literature and internet advertised hunts a further 20 species have been introduced (Chapter 3). Extraregional ungulate introductions have led to the differentiation of ungulate assemblages in South Africa due to different species being introduced to different places that have similar indigenous species assemblages (Chapter 2).
12. **Drivers:** At a provincial level, the number of extraregional ungulate species is positively related to the density of game farms (Chapter 2). At a QDGC resolution more extraregional ungulates have been introduced to areas of high human population numbers, high average annual income and high livestock numbers. However, 30-40 years ago more extraregional introductions were made to areas that are species poor for ungulates and had low numbers of livestock (Chapter 2) indicating that ungulates were introduced to increase species available for hunting, and to increase financial viability in marginal areas (Castley *et al.*, 2001; Lindsey *et al.*, 2006).
13. **Pathways:** In South Africa, zoological institutions have been responsible for several extraregional ungulate introductions (Chapter 3) following a global trend of this nature (Chapter 2). In the 20 year period, 1987-2006, 500 individuals of 19 extraregional ungulate species were sold or traded from zoological institutions in South Africa to non-zoo recipients (Chapter 3).
14. **Impacts:** In South Africa, unpublished studies have documented vegetation damage and soil erosion by *Hemitragus jemlahicus* (P.H. Lloyd, 1975) and two unpublished reports document the diet of *Sus scrofa* and damage to agricultural areas and relatively

untransformed habitat (J.H. Westdyk, 2000; D.L. Hignett, 2006). There doesn't seem to be any work documenting realized impacts of the most widely introduced extraregional ungulate species, fallow deer, *Dama dama*, and lechwe, *Kobus leche*. However, *Dama dama* populations are reportedly expanding and spreading. They have spread into a provincial nature reserve in the Free State of South Africa, where they are continuously controlled by culling (Watson, 2006). The paucity of evidence for the impacts of non-indigenous ungulates on biodiversity is not unique to South Africa, but is a problem globally (Chapter 5).

15. **Recommendations:** Information on extraregional species in South Africa that would be useful includes establishment success, extent of occurrence, population numbers, rates of spread and demonstrated impacts on biodiversity. Important in the demonstration of impacts on biodiversity is that studies ensure that the evidence obtained sufficiently demonstrates an impact, including the demonstration of population declines of indigenous species as a result of impacts from non-indigenous ungulates (Chapter 5). This is best achieved through field experiments such as by the use replicated exclosures (Chapter 5). *Dama dama* and *Sus scrofa* are apparently invasive in South Africa and are continually culled in some areas by farmers and reserve managers (Watson, 2006). *Sus scrofa* is a particularly problematic introduced ungulate globally, but little is known of the impacts of *Dama dama* (Chapter 5). Records of the number of individuals shot annually would be useful to indicate the population dynamics and spread of species like *Dama dama* and *Sus scrofa*. The impacts of *Dama dama* on vegetation and its competitive ability with indigenous species would also be useful to determine whether it is a threat to biodiversity. Anecdotal evidence suggests that scimitar-horned oryx, *Oryx dammah*, has hybridised with gemsbok, *Oryx gazella* and alleged hybrids have been shot by nature conservation authorities. Information on the incidence of hybridization between these species as well as the fertility of hybrids would be useful to determine how much of a threat scimitar-horned oryx poses to gemsbok. It is unlikely that landowners responsible for the introduction of extraregional species are going to take on the responsibility of controlling or removing them, especially if the animals were introduced many years ago. It may therefore be advisable to determine a certain level of risk at which extraregional species should be actively removed.

EXTRALIMITAL INTRODUCTIONS

16. **Policy:** As above, NEMBA restricts the movement of indigenous species outside their 'historical' distribution ranges without a permit and the granting of a permit requires a risk assessment (Anonymous, 2004).
17. **Extent:** According to advertisements in *Landbou Weekblad* all indigenous ungulate species in South Africa have been introduced extralimitally and translocations of up to c. 1600 km have significantly increased the range sizes of ungulate species. Introductions have increased through time and recently have been prominent in areas with high human population density (Chapter 3). As a consequence of numerous translocations, extralimital ungulates can be found in 264 QDGCs in South Africa (Chapter 3) and have lead to the homogenization of ungulate assemblages in these areas (Chapter 2). These ungulate assemblages have become more similar through time (1965-2005) with increasing extralimital introductions (Chapters 2 & 3) and extralimital introductions have homogenized ungulate assemblages to a greater degree than extraregional introductions have differentiated them.
18. **Drivers:** At a QDGC resolution more extralimital ungulates have been introduced to areas of low indigenous ungulate species-richness, high human population density and high livestock numbers i.e. areas that are productive, wealthy and species poor for ungulates (as would be expected based on the pool of ungulates extralimital to species poor areas), than to other areas (Chapter 2). Once the species pool available for introduction to each QDGC is controlled for, relatively more extralimital species than expected are introduced to areas that have higher indigenous ungulate species richness.
19. **Impacts:** Extralimital ungulates can impact floras through herbivory, they can compete with indigenous species through exploitation and habitat change, introduce novel pathogens and parasites and hybridize with indigenous ungulate species. Anecdotal evidence suggests competition between bushbuck, *Tragelaphus scriptus*, and nyala, *Tragelaphus angasii*, in areas in KwaZulu Natal where nyala occurs extralimitally (Coates & Downs, 2005). Giraffe, *Giraffa camelopardalis*, have significantly altered tree abundance and composition in their extralimital range in KwaZulu Natal (Bond & Loffell, 2001) and in the Eastern Cape this species has successfully established and browses a number of plant species (Parker & Bernard, 2005). Hybridization between blue wildebeest, *Connochaetes taurinus*, and black wildebeest, *Connochaetes gnou*, has been inferred where *C. taurinus* occurs

extralimitally (Fabricius *et al.*, 1988; Grobler *et al.*, 2005a). Inferences have been made that the translocation of springbok, *Antidorcas marsupialis*, extralimitally introduced a lungworm (*Bronchonema magna*), which then infested bontebok, *Damaliscus pygargus pygargus*, contributing to mortality (Meltzer, 1993). There are reports of extralimitally introduced warthog, *Phacochoerus africanus*, becoming problematic in the Eastern Cape, where they invaded Thomas Baines Nature Reserve and attempts of removal failed (Somers & Fike, 1993). However, no impacts of warthog have been quantified in the scientific literature and there appears to be nothing published on the impacts of the most common and potentially harmful extralimital introductions such as that of impala, *Aepyceros melampus*.

20. **Recommendations:** The translocation of ungulate species extralimitally could be particularly problematic. A large number of translocations have already brought conspecifics that could hybridize into close proximity, and in some cases onto the same properties (Chapter 3). Such introductions should be strictly prohibited to prevent introgression, which can result in extinction (Rhymer & Simberloff, 1996). Those conspecifics for which introgression is a threat should be identified and evidence of fertile first generation hybrids established using molecular techniques. Competition between indigenous and extralimital species has been suggested, but more investigation is required. Some impacts of extralimital species on vegetation have been shown (Bond & Loffell, 2001), but more information is required for other extralimital species and for the indirect effects the modification of vegetation will have on other species.

TRANSLOCATION PRACTICES WITHIN SPECIES

21. **Policy:** NEMBA restricts the movement of indigenous species between ‘population ranges’ (see Anonymous, 2007) without a permit and the granting of a permit requires a risk assessment (Anonymous, 2004). As very little molecular data are available for South African ungulates the ‘population ranges’ were designated by mammal experts. Parameters such as behaviour, ecoregions and perceived barriers to each species were used (P.H. Lloyd, pers. comm. 2008).
22. **Extent:** All indigenous ungulate species have been advertised for sale in *Landbou Weekblad* and comprise the majority of game and hunt advertisements (Chapter 3). Like other introductions, the number of indigenous ungulate species advertisements has also increased through time.

23. **Impacts:** The distances that ungulate species have been moved in South Africa i.e. across the entire country (mean: 490 ± 18 km) are likely to have led to genetic homogenization in ungulate species. Translocations of indigenous species may also introduce novel pathogens and parasites from other areas. Translocations of indigenous species have led to hybridization between subspecies e.g. between bontebok, *Damaliscus pygargus pygargus* and blesbok, *Damaliscus pygargus phillipsi* (Fabricius *et al.*, 1989) and Braack *et al.* (1995) have shown that non-indigenous parasites such as the tick *Rhipicephalus maculatus* were introduced to the Kruger National Park with the reintroduction of ungulates from elsewhere in South Africa.
24. **Surrogates for genetic distinctiveness:** In the absence of molecular data to designate genetically distinct populations in ungulate species other factors such as geomorphology and vegetation barriers could be useful (Chapter 4).
- a. Decision-makers in the past have used subspecies boundaries as guidelines for the restriction of translocations in South Africa (Lloyd & Lensing, 1990), but subspecies designations are not always supported by molecular data (Chapter 4).
 - b. Geomorphology may be useful in indicating areas of vicariance in ungulates (Cotterill, 2003), for example there is evidence that the East African rift valley and the Niger river, Nile river and Congo river may be important in vicariance elsewhere in Africa (Chapter 4), but for southern Africa evidence for faults and rivers in vicariance is limited and these features are smaller, or have not been stable for as long as topography elsewhere in Africa (Rautenbach *et al.*, 1979; Partridge & Maud, 1987; Partridge *et al.*, 1995).
 - c. Vegetation barriers are also important in the vicariance of ungulates e.g. disjunct arid zone distributions are observed between southern and eastern Africa (Roberts, 1937; Meester, 1965; Coe & Skinner, 1993). *Equus zebra* subspecies show a break in their distribution across the 'Knersvlakte' (a 70km wide waterless plain) and molecular data supports population structuring across this divide (Moodley & Harley, 2005). The isolation of habitat during Pleistocene climatic changes could also have been important in vicariance in South Africa (Partridge *et al.*, 1995). At the end of the tertiary, southern Africa was very arid and the savanna zone was restricted (Bond, 1963) but later during the Pleistocene, climatic conditions favouring the spread of forests occurred intermittently resulting in a more continuous forest belt than is currently observed (Meester, 1965).

d. Ecoregions have been suggested as a surrogate for genetic distinctiveness in Africa (Moodley & Bruford, 2007), but limited support has been found for them (Chapter 4).

e. Molecular studies conducted in South Africa on other taxa indicate that geomorphology and climate change (and resultant vegetation changes) are likely to have played a role in vicariance. Drainage systems are important in the vicariance of plants in South Africa (Ellis *et al.*, 2007). The 'Knersvlakte' (associated with the great western escarpment uplift) could be important in the vicariance of lizards (Matthee & Flemming, 2002) and shrews (Smit *et al.*, 2007). The reduction of forest and the development of fynbos, associated with climatic changes, are thought to have caused vicariance in chameleons (Tolley *et al.*, 2006). Price *et al.* (2007) found genetic differences between coastal regions (see Tinley, 1985) and between coastal and mountainous populations of cicadas, and scrub hares show three distinct populations in South Africa: the south western and central populations are particularly different and this has been attributed to zoogeographic barriers to dispersal (Kryger *et al.*, 2004). However, ungulates are much larger animals with dispersal abilities incomparable to most of these taxa.

25. **Recommendations:** Molecular work on the genetic structuring of ungulate species is imperative; although such work may demonstrate population structuring has already been lost. In which case it will be important to investigate how translocations have influenced genetic diversity in ungulate species in South Africa. Based on molecular work conducted elsewhere in Africa it is important that translocations of species from east and west Africa into South Africa are prohibited (Chapter 4) and it is possible that even translocations from neighbouring countries could be problematic (e.g. Grobler *et al.*, 2005b). Concerns for long distance translocations not only include the potential for genetic homogenization but also for the introduction of pathogens and parasites from other regions (see Meltzer, 1993).

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Appendix

Table 1. Presence of significant population structuring (SPS) in global ungulate species.

Species	SPS	References on population structure for species
<i>Aepyceros melampus</i>	Y	Nersting & Arctander, 2001; Lorenzen <i>et al.</i> , 2006a
<i>Alcelaphus buselaphus</i>	Y	Arctander <i>et al.</i> , 1999; Flagstad <i>et al.</i> , 2000
<i>Alces alces</i>	Y	Udina <i>et al.</i> , 2002
<i>Alces americanus</i>	Y	Broders <i>et al.</i> , 1999; Hundertmark <i>et al.</i> , 2002, 2003, 2006; Wilson <i>et al.</i> , 2003
<i>Antilocapra americana</i>	Y	Lee <i>et al.</i> , 1994; Stephen <i>et al.</i> , 2005
<i>Bison bison</i>	S	Polziehn <i>et al.</i> , 1996; Wilson & Strobeck, 1999
<i>Blastocerus dichotomus</i>	S	de Oliveira <i>et al.</i> , 2005; Marquez <i>et al.</i> , 2006
<i>Bubalus bubalis</i>	Y	Barker <i>et al.</i> , 1997a,b
<i>Budorcas taxicolor</i>	Y	Li <i>et al.</i> , 2003
<i>Capreolus capreolus</i>	Y	Randi <i>et al.</i> , 2004; Milosevic-Zlatanovic <i>et al.</i> , 2005; Lorenzini & Lovari, 2006; Zannese <i>et al.</i> , 2006; Royo <i>et al.</i> , 2007
<i>Capreolus pygargus</i>	Y	Tokarskaya <i>et al.</i> , 2000
<i>Cervus elaphus</i>	Y	Polziehn <i>et al.</i> , 2000; Corn & Nettles, 2001; Mahmut <i>et al.</i> , 2002; Hartl <i>et al.</i> , 2003, 2005; Ludt <i>et al.</i> , 2004; Hmwe <i>et al.</i> , 2006
<i>Cervus nippon</i>	Y	Goodman <i>et al.</i> , 2001; Lu <i>et al.</i> , 2006; Yuasa <i>et al.</i> , 2007
<i>Connochaetes taurinus</i>	Y	Arctander <i>et al.</i> , 1999
<i>Damaliscus lunatus</i>	S	Arctander <i>et al.</i> , 1999
<i>Damaliscus pygargus</i>	Y	Bigalke <i>et al.</i> , 1995
<i>Diceros bicornis</i>	Y	Swart & Ferguson, 1997; Harley <i>et al.</i> , 2005
<i>Equus zebra</i>	Y	Moodley & Harley, 2005
<i>Gazella gazella</i>	?	Vassart <i>et al.</i> , 1995
<i>Giraffa camelopardalis</i>	Y	Brown <i>et al.</i> , 2007
<i>Hippopotamus amphibius</i>	Y	Okello, 2005
<i>Hippotragus equinus</i>	Y	Matthee & Robinson, 1999; Alpers <i>et al.</i> , 2004

Table 1. continued.

Species	SPS	References on population structure for species
<i>Hippotragus niger</i>	Y	Matthee & Robinson, 1999; Pitra <i>et al.</i> , 2002
<i>Hydropotes inermis</i>	S	Hu <i>et al.</i> , 2006
<i>Kobus ellipsiprymnus</i>	Y	Lorenzen <i>et al.</i> , 2006b
<i>Kobus kob</i>	Y	Birungi & Arctander, 2000; Lorenzen <i>et al.</i> , 2007
<i>Muntiacus crinifrons</i>	Y	Wu <i>et al.</i> , 2006
<i>Nanger granti</i>	Y	Arctander <i>et al.</i> , 1996; Lorenzen <i>et al.</i> , 2008
<i>Odocoileus virginianus</i>	Y	Leberg & Ellsworth, 1999; DeYoung <i>et al.</i> , 2003; Moscarella <i>et al.</i> , 2003
<i>Ovis ammon</i>	N	Tserenbataa <i>et al.</i> , 2004
<i>Ovis canadensis</i>	S	Luikart & Allendorf, 1996; Boyce <i>et al.</i> , 1999
<i>Ovis dalli</i>	Y	Worley, 2004
<i>Ozotoceros bezoarticus</i>	Y	Gonzalez <i>et al.</i> , 1998
<i>Pantholops hodgsonii</i>	N	Ruan <i>et al.</i> , 2005
<i>Pecari tajacu</i>	Y	Gonogora <i>et al.</i> , 2006
<i>Phacochoerus africanus</i>	Y	Muwanika <i>et al.</i> , 2003, 2007
<i>Procapra picticaudata</i>	Y	Zhang & Jiang, 2006
<i>Procapra przewalskii</i>	Y	Lei <i>et al.</i> , 2003
<i>Pseudois nayaur</i>	Y	Wang <i>et al.</i> , 2006
<i>Rangifer tarandus</i>	Y	Cronin <i>et al.</i> , 2005
<i>Rhinoceros sondaicus</i>	Y	Fernando <i>et al.</i> , 2006
<i>Rucervus eldii</i>	Y	Balakrishnan <i>et al.</i> , 2003
<i>Rupicapra pyrenaica</i>	Y	Perez <i>et al.</i> , 2002
<i>Rupicapra rupicapra</i>		Perez <i>et al.</i> , 1996
<i>Sus scrofa</i>	Y	Watanobe <i>et al.</i> 1999, 2003
<i>Syncerus caffer</i>	Y	O’Ryan <i>et al.</i> , 1998; Wenink <i>et al.</i> , 1998; Simonsen <i>et al.</i> , 1998; van Hooft <i>et al.</i> , 2000, 2002, 2003
<i>Tapirus bairdii</i>	Y	Norton & Ashley, 2004
<i>Tragelaphus angasii</i>	Y	Grobler <i>et al.</i> , 2005
<i>Tragelaphus scriptus</i>	Y	Moodley & Bruford, 2007
<i>Tragelaphus strepsiceros</i>	Y	Nersting & Arctander, 2001
<i>Vicugna vicugna</i>	Y	Sarno <i>et al.</i> , 2004

Y, yes; N, no; S, some

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Table 2. Hybrids recorded in the literature and whether or not fertility was established: a) intra-genera: fertile, b) intra-genera: sterile or fertility unknown, c) Inter-genera: fertile, d) Inter-genera: sterile or fertility unknown

a) Intra-genera: fertile	References
<i>Bison bison</i> x <i>Bison bonasus</i>	Gray, 1972
<i>Bos frontalis</i> x <i>Bos grunniens</i>	Gray, 1972
<i>Camelus bactrianus</i> x <i>Camelus dromedarius</i>	Gray, 1972; Kohler-Rollefson, 1991
<i>Capra caucasica</i> x <i>Capra hircus</i>	Gray, 1972
<i>Capra falconeri</i> x <i>Capra hircus</i>	Gray, 1972
<i>Capra hircus</i> x <i>Capra ibex</i>	Turcek, 1951; Gray, 1972; Lever, 1994
<i>Cervus elaphus</i> x <i>Cervus nippon</i>	Donne, 1924; Delap, 1967; Gray, 1972; Harrington, 1973; Lowe & Gardiner, 1975; Lever, 1977; Harrington, 1982; Lever, 1985; Abernathy, 1994; Lever, 1994; Muir <i>et al.</i> , 1997; Goodman <i>et al.</i> , 1999; Diaz <i>et al.</i> , 2006;
<i>Connochaetes gnou</i> x <i>Connochaetes taurinus</i>	Gray, 1972; Fabricius <i>et al.</i> , 1988; Grobler <i>et al.</i> , 2005
<i>Equus asinus</i> x <i>Equus burchellii</i>	Gray, 1972
<i>Gazella bennettii</i> x <i>Gazella saudiya</i>	Gray, 1972; Kumamoto <i>et al.</i> , 1995; Rebholz & Harley, 1997
<i>Kobus ellipsiprymnus</i> x <i>Kobus megaceros</i>	Gray, 1972
<i>Muntiacus muntjak</i> x <i>Muntiacus reevesi</i>	Gray, 1972
<i>Odocoileus hemionus</i> x <i>Odocoileus virginianus</i>	Cowan, 1962; Gray, 1972; Wishart, 1980; Anderson & Wallmo, 1984; Carr <i>et al.</i> , 1986; Stubblefield <i>et al.</i> , 1986; Ballinger <i>et al.</i> , 1992; Carr & Hughes, 1993; Hornbeck & Mahoney, 2000
<i>Oryx beisa</i> x <i>Oryx gazella</i>	Gray, 1972
<i>Oryx dammah</i> x <i>Oryx leucoryx</i>	Gray, 1972
<i>Ovis ammon</i> x <i>Ovis aries</i>	Gray, 1972
<i>Ovis ammon</i> x <i>Ovis canadensis</i>	Gray, 1972
<i>Ovis aries</i> x <i>Ovis canadensis</i>	Gray, 1972
<i>Sus barbatus</i> x <i>Sus scrofa</i>	Gray, 1972; Oliver <i>et al.</i> , 1993; Mungall & Sheffield, 1994
<i>Tragelaphus eurycerus</i> x <i>Tragelaphus spekii</i>	Gray, 1972; Koulischer, Tijsskens & Mortelmans, 1973

Table 2. continued.

b) Intra-genera: sterile or fertility unknown	
<i>Axis axis x Axis porcinus</i>	Gray, 1972
<i>Bos frontalis x Bos javanicus</i>	Gray, 1972
<i>Bos frontalis x Bos taurinus</i>	Gray, 1972; Lenstra & Bradley, 1999
<i>Bos grunniens x Bos taurinus</i>	Gray, 1972; Lenstra & Bradley, 1999
<i>Bos javanicus x Bos taurinus</i>	Gray, 1972; Nijman <i>et al.</i> , 2003
<i>Capra caucasica x Capra ibex</i>	Gray, 1972
<i>Capra caucasica x Capra sibirica</i>	Gray, 1972
<i>Capra falconeri x Capra ibex</i>	Gray, 1972
<i>Capra falconeri x Capra nubiana</i>	Gray, 1972
<i>Capra hircus x Capra nubiana</i>	Gray, 1972
<i>Capra hircus x Capra sibirica</i>	Gray, 1972; Mungall & Sheffield, 1994
<i>Capreolus capreolus x Capreolus pygargus</i>	Gray, 1972
<i>Cephalophus dorsalis x Cephalophus rufilatus</i>	Gray, 1972
<i>Cephalophus dorsalis x Cephalophus zebra</i>	Gray, 1972
<i>Equus asinus x Equus caballus</i>	Gray, 1972
<i>Equus asinus x Equus grevyi</i>	Gray, 1972
<i>Equus asinus x Equus hemionus</i>	Gray, 1972
<i>Equus asinus x Equus kiang</i>	Gray, 1972
<i>Equus asinus x Equus zebra</i>	Gray, 1972
<i>Equus burchellii x Equus caballus</i>	Gray, 1972
<i>Equus burchellii x Equus grevyi</i>	Gray, 1972; Mungall & Sheffield, 1994
<i>Equus burchellii x Equus hemionus</i>	Gray, 1972
<i>Equus burchellii x Equus kiang</i>	Gray, 1972
<i>Equus burchellii x Equus zebra</i>	Gray, 1972
<i>Equus caballus x Equus grevyi</i>	Gray, 1972
<i>Equus caballus x Equus hemionus</i>	Gray, 1972
<i>Equus caballus x Equus kiang</i>	Gray, 1972
<i>Equus caballus x Equus zebra</i>	Gray, 1972
<i>Equus grevyi x Equus zebra</i>	Gray, 1972
<i>Equus hemionus x Equus kiang</i>	Gray, 1972
<i>Equus hemionus x Equus zebra</i>	Gray, 1972
<i>Eudorcas rufifrons x Eudorcas thomsonii</i>	Gray, 1972
<i>Gazella arabica x Gazella gazella</i>	Gray, 1972
<i>Gazella dorcas x Gazella gazella</i>	Mendelssohn <i>et al.</i> , 1995
<i>Gazella gazella x Gazella subgutturosa</i>	Mendelssohn <i>et al.</i> , 1995
<i>Gazella leptoceros x Gazella subgutturosa</i>	Gray, 1972

Table 2. continued.

b) Intra-genera: sterile or fertility unknown	
<i>Hippotragus equinus x Hippotragus niger</i>	Robinson & Harley, 1995
<i>Kobus ellipsiprymnus x Kobus kob</i>	Gray, 1972
<i>Kobus kob x Kobus megaceros</i>	Gray, 1973
<i>Kobus leche x Kobus megaceros</i>	Gray, 1972
<i>Madoqua guentheri x Madoqua kirkii</i>	Kingdon 1982; Kingswood & Kumamoto, 1997
<i>Mazama americana x Mazama nana</i>	Duarte & Jorge, 2003
<i>Naemorhedus goral x Naemorhedus griseus</i>	Gray, 1972
<i>Oryx beisa x Oryx dammah</i>	Mungall & Sheffield, 1994
<i>Oryx beisa x Oryx lecoryx</i>	Mungall & Sheffield, 1994
<i>Oryx dammah x Oryx gazella</i>	CapeNature
<i>Philantomba maxwellii x Philantomba monticola</i>	Gray, 1972
<i>Rusa alfredi x Rusa unicolor</i>	Gray, 1972
<i>Rusa timorensis x Rusa unicolor</i>	Bentley, 1978; Lever, 1994
<i>Sus celebensis x Sus scrofa</i>	Macdonald, 1993
<i>Sus philippensis x Sus scrofa</i>	Oliver <i>et al.</i> , 1993
<i>Sus scrofa x Sus verrucosus</i>	Blouch, 1995
<i>Tapirus bairdii x Tapirus terrestris</i>	Padilla & Dowler, 1994
<i>Tragelaphus angasii x Tragelaphus spekii</i>	Mungall & Sheffield, 1994
<i>Tragelaphus imberbis x Tragelaphus spekii</i>	Gray, 1972
<i>Tragelaphus scriptus x Tragelaphus spekii</i>	Gray, 1972
<i>Tragelaphus spekii x Tragelaphus strepsiceros</i>	Mungall & Sheffield, 1994
c) Inter-genera: fertile	
<i>Axis axis x Cervus elaphus</i>	Gray, 1972; Mungall & Sheffield, 1994
<i>Bison bison x Bos grunniens</i>	Gray, 1972
<i>Bison bison x Bos taurinus</i>	Gray, 1972
<i>Cervus elaphus x Elaphurus davidianus</i>	Gray, 1972; Goosen <i>et al.</i> , 1999
<i>Cervus elaphus x Przewalskium albirostris</i>	Environment and Development Desk, 2005
<i>Lama glama x Vicugna vicugna</i>	Gray, 1972
d) Inter-genera: sterile or fertility unknown	
<i>Addax nasomaculatus x Oryx dammah</i>	Mungall & Sheffield, 1994
<i>Addax nasomaculatus x Oryx gazella</i>	Mungall & Sheffield, 1994
<i>Addax nasomaculatus x Oryx lecoryx</i>	Mungall & Sheffield, 1994
<i>Alcelaphus caama x Damaliscus lunatus</i>	Gray, 1972
<i>Alcelaphus caama x Damaliscus pygargus</i>	Kettlitz, 1967; Gray, 1972; Robinson <i>et al.</i> , 1991
<i>Ammotragus lervia x Capra hircus</i>	Gray, 1972

Table 2. continued.

d) Inter-genera: sterile or fertility unknown	
<i>Antilope cervicapra x Eudorcas thomsonii</i>	Mungall & Sheffield, 1994
<i>Antilope cervicapra x Gazella bennettii</i>	Mungall & Sheffield, 1994
<i>Axis axis x Cervus nippon</i>	Asher <i>et al.</i> , 1999
<i>Axis axis x Odocoileus virginianus</i>	Gray, 1972
<i>Axis axis x Rucervus duvaucelii</i>	Gray, 1972
<i>Axis porcinus x Capreolus capreolus</i>	Gray, 1972
<i>Axis porcinus x Dama dama</i>	Gray, 1972
<i>Cephalophus nigrifrons x Sylvicapra grimmia</i>	Gray, 1972
<i>Ceratotherium simum x Diceros bicornis</i>	Robinson <i>et al.</i> , 2005
<i>Cervus elaphus x Alces alces</i>	Gray, 1972
<i>Cervus elaphus x Odocoileus hemionus</i>	Gray, 1972; Mungall & Sheffield, 1994
<i>Cervus elaphus x Rangifer tarandus</i>	Gray, 1972
<i>Cervus elaphus x Rusa timorensis</i>	Asher <i>et al.</i> , 1999
<i>Dama dama x Odocoileus hemionus</i>	Mungall & Sheffield, 1994
<i>Gazella thomsoni x Eudorcas rufifrons</i>	Gray, 1972
<i>Pecari tajacu x Tayassu pecari</i>	Zuckerman, 1953; Gray, 1972; Sowls, 1984
<i>Potamochoerus larvatus x Sus scrofa</i>	Vercammen <i>et al.</i> , 1993
<i>Potamochoerus porcus x Sus scrofa</i>	Vercammen <i>et al.</i> , 1993
<i>Taurotragus oryx x Tragelaphus strepsiceros</i>	Gray, 1972

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Figure 1. Ungulate sister-species distributions with estimated date of divergence from Hernández Fernández & Vrba (2005) (million years ago (mya)).

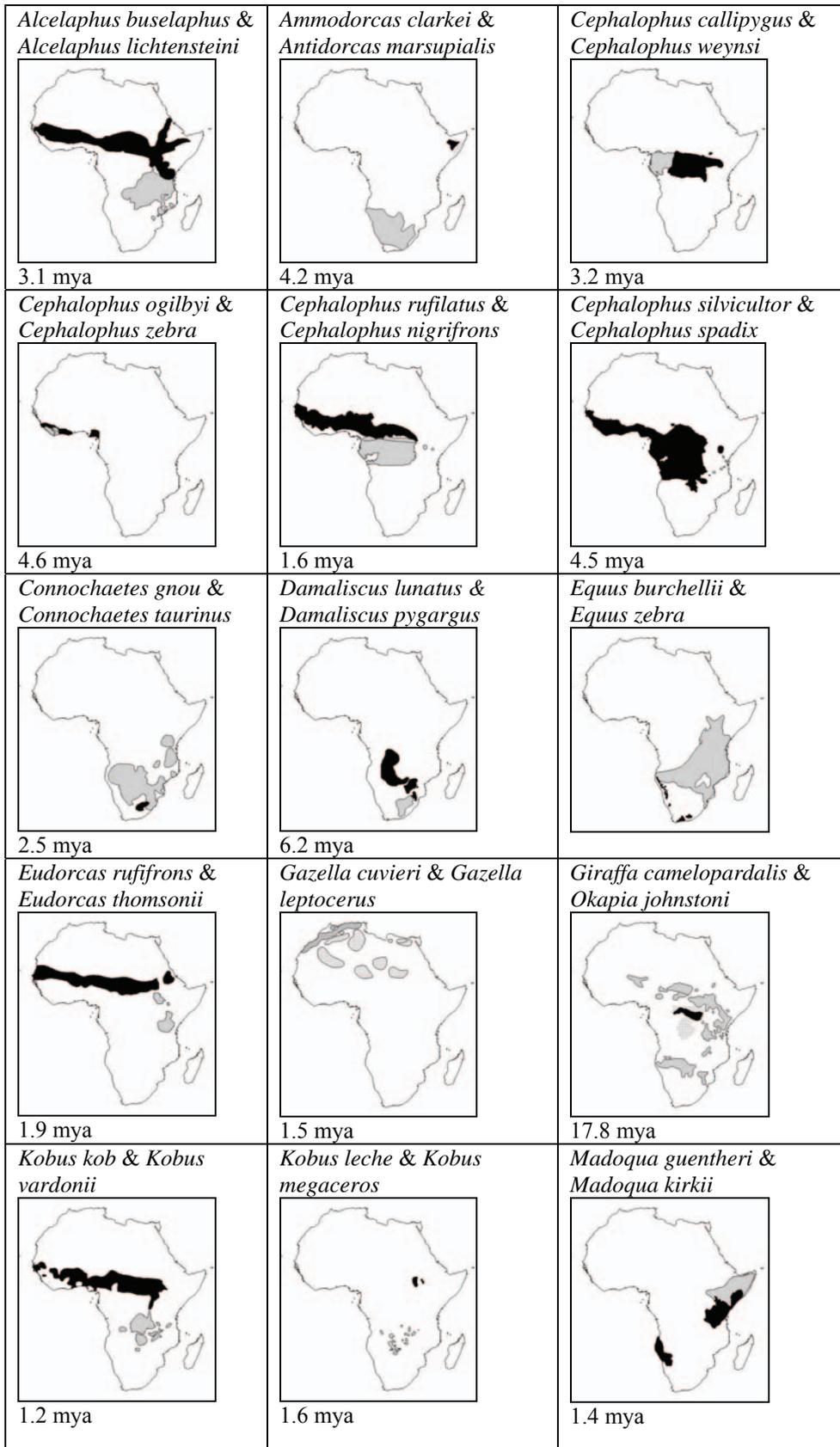
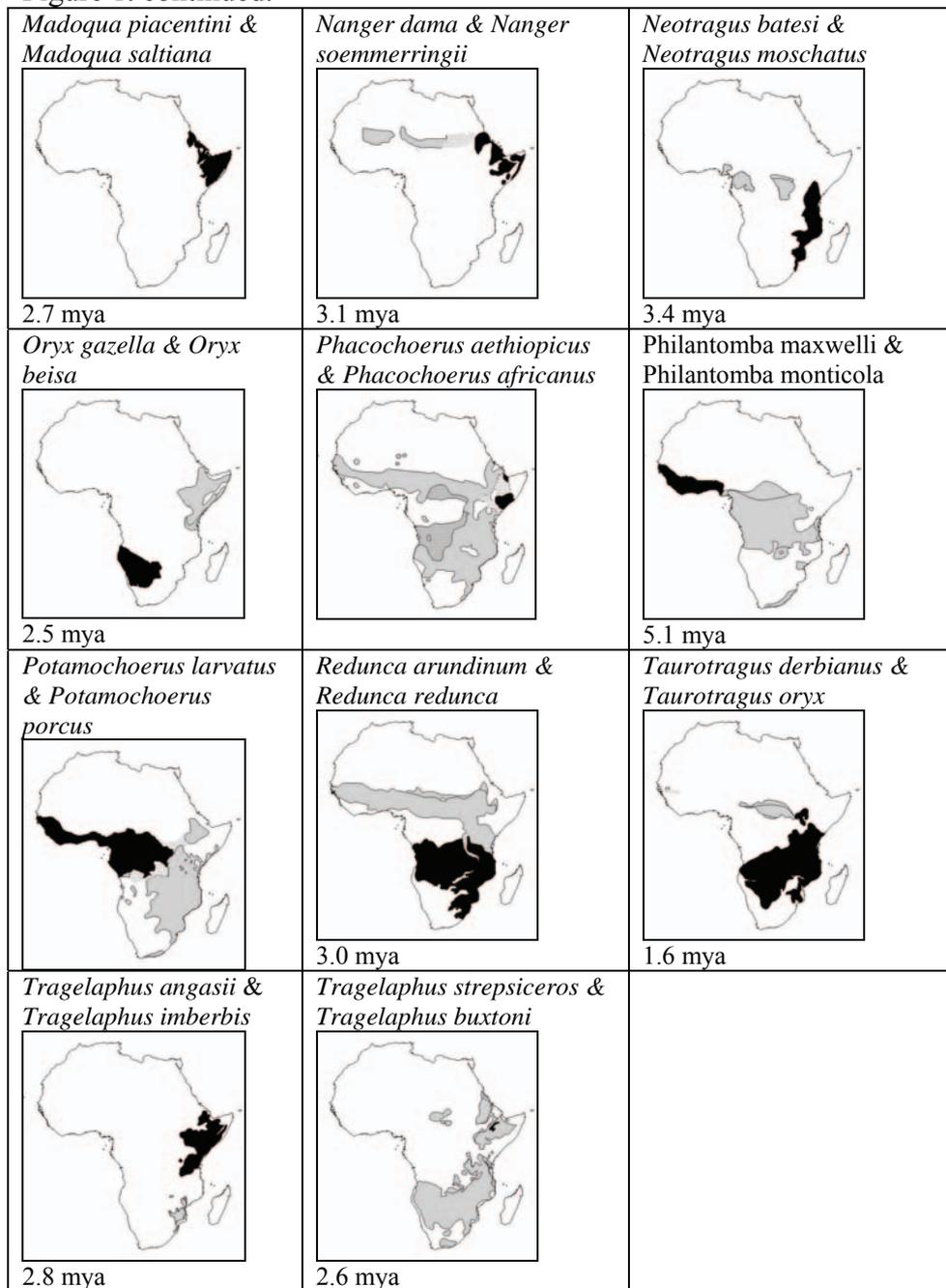


Figure 1. continued.



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