MAMMALIAN AND AVIAN DIVERSITY IN A COASTAL NATURE RESERVE AND AN ADJACENT ECO-ESTATE

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ABSTRACT

The burgeoning human population is placing increasing pressure on natural resources, including undeveloped land, for a variety of human activities including residential housing. Despite making up only a small percentage (5.4 %) of transformed land, urban areas have had a disproportionate impact on biodiversity with many cities having been founded in biodiversity hotspots at the confluence of marine, freshwater and terrestrial ecosystems. A growing trend worldwide and particularly in countries with a large wealth gap is the development of low density private residential estates. Although primarily conceived to improve home security, private estates are nevertheless regarded as a form of geographical escapism, and they are increasingly being marketed as eco- and lifestyle estates. While no formal definition of an eco-estate exists nor what ecological criteria must be satisfied to qualify for the status of an "ecological estate," increasingly such estates make bold claims concerning their contributions to the conservation of native flora and fauna. Currently, little is known about the impacts of eco-estates on the ecology and wildlife of an area, particularly when compared to natural land. To date, most research on estates has focused on comparing their impact with transformed, agricultural or even urban land uses. In this study I compare select elements of the fauna within a golfing eco-estate (Atlantic Beach Estate), located 25 km north of Cape Town to the neighbouring Blaauwberg Nature Reserve, from which the estate was originally cleaved.

I used live trapping, camera trapping and point counts for small mammals, medium/large mammals and birds respectively to compare the fauna in both the estate and reserve. For birds I was able to include a before and after comparison with a similar study in the early phases of the estate's development. All fieldwork was conducted between September and November 2019.

Small mammal diversity was similar within the estate and the reserve, but the former included an exotic invasive (the house rat (*Rattus rattus*)) while the latter supported the vulnerable white-tailed rat (*Mystromys albicaudatus*). Medium sized mammal species composition varied significantly between the estate and reserve with the latter having more native species and the estate having three domestic species in addition to an introduced, extralimital wild species, the springbok (*Antidorcas marsupialis*). Bird communities were similar, with marked overlap in species between the two land uses. The addition of permanent water and private gardens with both native and non-native flora has increased both the niche breadth and food availability within the estate which was reflected in a higher avian diversity than in the neighbouring, more homogenous, reserve. In addition to supporting almost all the species found in the reserve, the estate was able to support multiple fynbos-endemic species not found in the nature reserve, as well as species closely associated with water. The presence of the eco-estate does not appear to have negatively impacted the bird community as the additional resources provided by the estate allow both urban exploiters and urban tolerators/avoiders to persist.

In summary the estate has adversely impacted medium sized mammals more than both small mammals and birds with the latter taxon arguably benefiting from the increased habitat heterogeneity. Improving medium sized mammal richness would require increasing the permeability of the estate boundary but this will compromise both the safety of residents from external human threats and mammals within the reserve from domestic animals originating from the estate. Restricting domestic animals to private property, eliminating exotic species, improving connectivity between patches of natural habitat and naturalizing the edges of the golf course are all attainable goals that may improve small mammal and bird communities within the estate. However medium and large mammals are seldom compatible with human habitation and are thus likely to be the faunal component most adversely impacted by eco-estates with their limited size and impermeable edges. Ultimately while eco-estates may offer habitat for some species, they are not uniformly suitable for all species, and particular attention must be given to characteristics of prevailing species which might preclude them from an estate before estate construction. Given the increasing popularity of eco-estates and increased pressure on wildlife these are important findings which can help improve conditions for wildlife on current eco-estates and help facilitate site selection for any future eco-estate construction.

DECLARATION

I, Michael Duncan Ross, hereby declare that this dissertation was carried out in accordance with the regulations of the University of Cape Town; that the work on which this dissertation is based is my original work (except when expressly indicated otherwise); and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree at this or any other university. I grant the university free license to reproduce this dissertation, in whole or in part, for research purposes. I am presenting this dissertation for examination towards the Degree of Master of Science in Biological Sciences.

This thesis has been submitted to the Turnitin module and I confirm that my supervisors have seen my report and that any concerns raised therefrom have been resolved between myself and my supervisors.

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The acknowledgements section of this dissertation has by far and away been my favourite section to write. Firstly, as I pen this section, the end is in sight. After a long journey, suddenly there appears to be light at the end of the tunnel and final submission seems within reach. At the end of a long journey, one invariably feels ready for the finish, despite the fun one has had along the way. Secondly, I feel somewhat less constrained by the rigours of scientific writing, and freer to express myself in a way which comes more naturally. Lastly, and most importantly, I have a chance to reflect on the important people who have played a role in helping this dissertation come to fruition.

There have been numerous people without whom this journey of mine would have been significantly more difficult, if not impossible. While I will recognize the main contributors here, this unfortunately neglects everyone else with little contributions along the way. They have meant more than any of you will ever know. Cumulatively, these encouraging words or little acts of service have carried me through the challenging times and made the good times even more special. Since I started this project, I have had a sticky note placed at my desk which reads: “Moments matter. This moment matters.” Well-intentioned, well-timed, thoughtful words can make all the difference.

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For someone out there who needs to read this…

CHAPTER 1: Introduction

Background and context of the study

The human population has increased exponentially since the 1760s, which coincided with the Industrial Revolution (*United Nations World Population Prospects*, 2019). An increasing population requires more natural resources driving the conversion of natural habitat for anthropogenic land uses and depriving wildlife of critical resources (McKee *et al.*, 2004; Tilman *et al.*, 2017). Animals are consequently either forced into smaller protected areas, or persist in unprotected land, within both agricultural and urban settings that may result in regular interactions with humans (Nyhus, 2016). While some of these interactions may be positive for both people and wildlife (e.g., birds in residential gardens), many are negative often with severe consequences for people and wildlife (Hoffman and O'Riain, 2011; Redpath *et al.*, 2013; Beamish and O'Riain, 2014). Negative interactions require management interventions to reduce both the negative impacts of people (e.g., poor waste management) and wildlife (e.g., damage to property) and so restore balance to what are typically disrupted ecosystems that lack key elements such as apex predators (Soulsbury and White, 2015).

In general, urbanization results in simplified communities with reduced species richness and diversity as urban landscapes present unique challenges and opportunities to animals not found in a natural landscape (Chace and Walsh, 2006; Beninde, Veith and Hochkirch, 2015). Species may be broadly classified as urban exploiters, urban tolerators or urban avoiders, based on their capacity to survive and thrive in urban environments (Blair, 1996; McKinney, 2002). Urban exploiters are usually adaptable generalist or opportunistic species that benefit from living in human-modified landscapes (McKinney, 2002). These species thrive in urban areas, and density of these species may be much higher than would be found in a natural environment because of plentiful food supplies, the absence of predators and access to roosting sites (McKinney, 2002). Indeed, some species rely heavily, and in some cases exclusively on humans for food (e.g., feral pigeons (*Columba livia domestica*)). Urban tolerators can persist in urban areas but receive no net benefit from humans. Finally, urban avoiders are unable to persist in an urban environment as they have very specific habitat requirements, require large tracts of natural land or come into conflict with humans (e.g., large carnivores) (McKinney, 2002; Nyhus, 2016).

More recently we are increasingly recognizing the importance of urban areas in wildlife conservation and gaining greater understanding about the drivers of species distribution patterns across urban spaces (Beninde, Veith and Hochkirch, 2015; Aronson *et al.*, 2017; Soanes and Lentini, 2019; Soanes *et al.*, 2019). There is growing recognition that urban areas are a mosaic, comprising many different patches, which vary in suitability for wildlife and are not necessarily equally suitable for wildlife, as some species persist better in more natural patches, while others thrive in human-dominated habitats (Maseko *et al.*, 2019; Zungu *et al.*, 2020; Downs *et al.*, 2021). In general, increasing patch area and patch connectivity increases biodiversity, provided the vegetation structure remains suitable (Beninde, Veith and Hochkirch, 2015). Importantly however, the inverse does not necessarily hold true – that small patches with suitable connectivity harbour limited biological diversity. Indeed small patches within an urban matrix can support remarkable diversity, which can, at times, be comparable to nonurban areas (Prugh *et al.*, 2008; Soanes *et al.*, 2019). Despite a tendency to focus only on large, well-connected natural areas, the general neglect of small habitat patches overlooks an important reservoir of biodiversity (Kendal *et al.*, 2017; Kowarik, 2018). As the urban matrix expands, the conservation of both large and small urban green space will become increasingly necessary (Goddard, Dougill and Benton, 2010). Species respond differently to urbanisation and that different landscape characteristics can suit some species while simultaneously adversely impacting others (Garden, McAlpine and Possingham, 2010; Fischer *et al.*, 2015).

The City of Cape Town is an excellent example of rapid human population growth, and resultant urban sprawl into natural areas. In 1950 there were approximately 742 400 people (Wilkinson, 2000). By 2019 this number had grown to over 4 600 000 people (Holmes *et al.*, 2012; Western Cape Government, 2020). Natural land has been developed mostly for housing and light industry, leaving only small patches of natural habitat in a patchwork of protected areas and green belts throughout the city (Schnetler, Radloff and O'Riain, 2020). Extensive tracts of natural land persist both within (e.g., Table Mountain National Park) and on the periphery of the City of Cape Town, bringing a range of wildlife into regular contact with residents. This includes chacma baboon (*Papio ursinus),* Cape porcupine (*Hystrix africaeaustralis*), Cape clawless otter (*Aonyx capensis*), Cape fur seal (*Arctocephalus pusillus*), mongoose (*Herpestidae* spp.), genet (*Genetta* spp.) and caracal (*Caracal caracal*) (Schnetler, Radloff and O'Riain, 2020). Pressure to develop this natural land remains high, given the continued growth of the population, and the large number of people living in informal townships without adequate infrastructure, resulting in 6.5 km^2 of land transformation for development every year (Rebelo *et al.*, 2011). Recently, large tracts of natural land have been ceded to upmarket developments including eco-estates that seek to preserve elements of the natural land within high end residential housing estates (Mistry and Spocter, 2020).

Gated communities, estates and eco-estates

A gated community is described as "a physical area that is fenced or walled off from its surroundings" (Landman and Badenhorst, 2012). The key characteristic of such a community is that a particular space becomes privatized with conditional entry (Landman and Badenhorst, 2012). The broad use of the term "gated community" means these communities can house a variety of different land use types.

Gated communities that protect upmarket residential developments are typically referred to as “estates” which I define as “an enclosed community where residential housing is one of its primary purposes.” All estates are gated communities, but not all gated communities are estates.

There are many different types of estates, each with different priorities, though similar in their focus on security (Lemanski, 2004). Fear of crime is thought to be driving the rapid growth in the number of estates around the world, especially in countries where crime is pervasive, often violent and impacts wealthy people directly (such as Brazil and South Africa) (Lemanski, 2004). Perhaps unsurprisingly, these countries have some of the highest Gini coefficients in the world (South Africa is ranked the most unequal country in the world) (*The World Bank Gini Index*, 2021). Estates are usually protected by specialized security companies, and as such the burden of protection lies upon their shoulders, relieving the community members of this duty and their reliance on the national police force (Lemanski, Landman and Durington, 2008). Private security personnel are often combined with electric fences, guard dogs and closed-circuit television cameras (Lemanski, Landman and Durington, 2008).

Although increasingly sought after, estates are highly contentious spaces. They have been criticized for their use of separation, exclusion and avoidance (Hook and Vrdoljak, 2001) and have been described as examples of “geographical escapism," in which residents seek to isolate themselves from the problems of the world surrounding them (Landman and Badenhorst, 2012). More than just geographically, estates practice self-governance, led by a democratically elected body corporate, and strive towards becoming a pseudo-independent state. Commercial hubs, schools, shops, recreational activities and other amenities found on many estates create a self-contained system minimizing reasons for residents to leave (Hook and Vrdoljak, 2001). Estates may therefore have a limited dependence on the external environment, and may be situated almost anywhere (Caldeira, 1996). Many of these estates have strict rules dictating resident’s behaviour, and architectural guidelines that produce a level of building conformity (Hook and Vrdoljak, 2001) - with the threat of expulsion should residents fail to comply. The high costs of purchasing property within an estate excludes most citizens, while visitors must satisfy a strict set of criteria before entry is permitted. Perceptually, there is a clear contrast which forms between the “safe inside” and the “dangerous outside” (Lemanski, Landman and Durington, 2008).

While the fear of crime is often publicly portrayed as the main reason for the creation of estates, this may mask other important drivers of the formation of such communities. Residents may be concerned about racial or social differences because human identity is shaped to some extent by community (Lemanski, 2004; Kriesberg, 2010). Living in close spatial proximity narrows the difference between those who are thought to belong, and those who do not, challenging an individual's identity and leading to feelings of anxiousness and unease. Estates thus maintain the social and spatial identity that classes have become accustomed to (Wilton, 1998).

These problems are magnified in South Africa, where many estates effectively recreate spatially discrete pockets of racially biased groups that the apartheid regime sought to enforce (Lemanski, Landman and Durington, 2008). In the post-apartheid South Africa, citizens are no longer divided geographically along racial lines, however economic status, class and race remain inextricably linked (Babarinde, 2009). The result is the (in)advertent creation of socially homogeneous communities, within geographically distinct suburbs ranging from extensive informal settlements to gated private estates (Lemanski, Landman and Durington, 2008). The latter are occupied by the minority of wealthy, mostly white citizens, while the former are largely occupied by the poor, mostly black citizens of the country (Lemanski, 2006).

In the face of growing criticism from as high up as the presidential office for reinforcing social inequality (Mbeki, 2005), estates have been forced to rebrand away from elite opulence and towards other labels, such as being environmental custodians (Ballard and Jones, 2011). Estates, and eco-estates in particular, are on the rise, offering both the lure of secure living accompanied by a close connection to nature (Sherriff-Shüping, 2015). In South Africa, no formal definition exists for the term "eco-estate" and there are no guidelines to distinguish an eco-estate from a security estate (Thambu, 2007). As a result different eco-estates display differing levels of "eco-ness" (Mistry and Spocter, 2020).

Eco-estates may be given permission to develop on ecologically sensitive land, because they purport to follow environmentally sensitive principles and practices, and may even claim to enhance degraded natural habitats, including wetlands (Mistry and Spocter, 2020, 2022). There is, however, mounting concern that eco-estates may be engaged in what has been termed "greenwashing," where developers understate the ecological impacts of the proposed development and triumph potential ecological benefits in the approval phase of the development (Athanasiou, 1996). Greenwashing, in essence, promises environmentally sound practices and outcomes, but these are seldom either quantified or realised. To qualify as greenwashing, Delmas and Burbano (2015) suggest two requirements: "poor environmental performance and positive communication about [proposed] environmental performance."

Golf courses have a much longer history than eco-estates and are widely regarded as one of the more nature friendly sports amongst the general public, and yet have been accused of greenwashing (Ceron-Anaya, 2010; Wheeler and Nauright, 2016). Golf courses are inextricably linked to the outdoors and nature and are generally situated amongst beautiful surroundings. The non-playing areas stand in stark contrast to the heavily human modified golf greens and fairways, which have been likened to green deserts that exclude most native flora and fauna. The grass monoculture is maintained through intensive irrigation, and heavy pesticide and fertilizer use, to produce a suitable playing surface (Wheeler and Nauright, 2016). Golf greens and fairways are thus only able to support depauperate faunal communities, while their maintenance has both upstream (e.g., lack of water) and downstream (e.g., eutrophication) impacts (Wheeler and Nauright, 2016). The significance of these claims cannot be understated because of the huge tracts of land occupied by golf courses. To put golf courses into perspective: globally, there are approximately 33 161 golf facilities (R&A, 2017) covering roughly 17 013 km^2, based on the estimate of an 18 hole golf course covering 54 ha (Terman, 1997). Most courses include between 25 % and 40 % non-playing area (Gange, Lindsay and Schofield, 2003) which is often fragmented natural vegetation.

There are two important questions to ask when considering the ecological value of a golf course. Perhaps the most important is: what habitat or land use type was present before the golf course was constructed (Colding and Folke, 2009)? As a sweeping generalization, golf courses are more suitable for wildlife than urban or agricultural land, but less suitable than natural land (Gange, Lindsay and Schofield, 2003; Tanner and Gange, 2005; Colding and Folke, 2009). Therefore, if a golf course replaces agricultural land, it is likely to host an increased number of species, with a more even spread of individuals among the species. Conversely, a golf course constructed in an area of natural land will drive a reduction in species diversity and evenness. Secondly: what type of golf course is planned? It is important to recognize that not all golf courses are equal. Different styles of golf course can have significantly different impacts on the local environment. Some golf courses (e.g., naturalistic golf courses) which retain significant tracts of natural land and control illegal activities such as poaching, can actually benefit wildlife populations (Terman, 1997; Tanner and Gange, 2005; Colding and Folke, 2009).

A growing trend in South Africa is the inclusion of golf courses within eco-estates to produce golfing eco-estates with both land uses claiming to practice environmentally sensitive principles and marketing themselves as havens for wildlife. However, as with eco-estates, there has been little research into the effect a golfing eco-estate might have on biological communities, and whether they can sustain biologically meaningful wildlife populations.

What species persist on golfing eco-estates?

Generally, golf courses (i.e., parts of a golf course most closely associated with playing golf such as the greens and fairways) are home to a characteristic suite of species. The heavily human modified conditions necessary to sustain a golf course mean that these parts of a golf course are similar, regardless of where the course is situated. Habitat types and species composition on golf courses hundreds of km apart, may more closely resemble one another than natural land adjacent to a golf course (Blair, 2001). Species which favour conditions on golf courses may be found well outside their distribution, because anthropogenic modification has created a suitable habitat patch (Blair, 2001). Such species are usually those which are adaptable generalists, opportunistic species or urban exploiters (McCleery, Moorman and Peterson, 2014). In southern Africa, golf courses have helped facilitate the range expansion of hadeda ibis (*Bostrychia hagedash*), a probe forager, by increasing soil moisture, through irrigation, and thereby foraging efficiency (Duckworth, Altwegg and Guo, 2010). Importantly golf courses do not comprise solely of greens and fairways. Similar to urban areas, golf courses comprise a mosaic of manicured greens and fairways but are often surrounded by important landscape features which retain biological diversity in patches of natural vegetation, and can indeed bolster it, when compared to other human-modified land, with the inclusion of features not found in the surrounding areas (e.g., water bodies) (Tanner and Gange, 2005; Colding and Folke, 2009). The extent to which this occurs is dependent upon the proportion of natural vegetation, which is the biggest predictor of species richness on course (Hodgkison, Hero and Warnken, 2007; Sorace and Visentin, 2007; Nooten *et al.*, 2018).

Peri-urban landscapes are a unique interface where indigenous, human-introduced and human companion animals interact (Shochat *et al.*, 2006). Urban exploiting species can typically extend their range into these human modified landscapes. These species may persist at high densities because of supplementary food and water. Depending on estate rules and regulations, humans may bring with them a suite of companion animals, including domestic cats (*Felis catus*) and dogs (*Canis lupus familiaris*). Cats in particular may have substantial impacts on the local biodiversity (Seymour *et al.*, 2020). Additionally, there are unintentional introductions of urban exploiting species, such as rats (*Rattus rattus* and *R. norvegicus*), which may predate on a variety of local fauna and outcompete naturally occurring small mammals. Furthermore, peri-urban landscapes may provide a haven for some animals, by excluding those which are not tolerated by humans (e.g., large carnivores).

Species composition within a community

Understanding the impacts of eco-estates and other urban land uses, such as golf courses, on wildlife communities ideally requires before and after studies. However, these are seldom achieved owing to the process of application and subsequent development typically being out of step with the planning, funding and execution of research studies. Furthermore, when seeking to understand the potential impacts of a change in land use it is seldom possible to include all elements of flora and fauna when assessing the impacts on biota. By sampling select functional groups, taxa or even species which to some degree represent the health of an entire ecosystem, we can make inferences about the impacts of developments on biodiversity and ecosystem health. Such species are known as indicator species and are defined as “an organism whose characteristics (e.g., presence or absence, population density, dispersion, reproductive success) are used as an index of attributes which may be too difficult, inconvenient or expensive to measure for other species or environmental conditions of interest” (Landres, Verner and Thomas, 1988). Hilty and Merenlender (2000) suggest 13 criteria which should guide selection of an indicator species. Birds (Gardner *et al.*, 2008) and small mammals (Avenant, 2000, 2011) fulfill many of these criteria and hence are routinely used, while mammals are less frequently used as indicators, but nevertheless remain worthy of study in this regard (Landres, Verner and Thomas, 1988). Such indicator species can be studied at the community level where a community consists of various interacting species residing in close geographic proximity (Krebs, 1972). A community can be quantified in terms of its constituent parts: its diversity and its evenness (how the number of individuals is divided among the number of species) (McCleery, Moorman and Peterson, 2014).

Gap in the market

In South Africa, as eco-estates become increasingly common, research on eco-estates is becoming more prevalent (Grey-Ross, Downs and Kirkman, 2009; Sherriff-Shüping, 2015; Alexander *et al.*, 2019c, 2019b, 2019a, 2021). Some research has centered on aspects of sustainability such as the utilisation of local building materials, recycling, efficient water use and renewable sources of energy (Sherriff-Shüping, 2015). While these are all important aspects of a green development, but they fail to address the impacts of such a development on the local fauna. Furthermore, some studies on fauna have typically focused on single species (e.g., oribi (*Ourebia ourebi*)) or members of a single class (e.g., Aves), limiting an understanding of community level impacts (Grey-Ross, Downs and Kirkman, 2009; Alexander *et al.*, 2019c). Multi-taxa research on eco-estate suitability in South Africa has been limited to Kwa-Zulu Natal, and has focused on the transition from agricultural land to that of an eco-estate with the conclusion that “eco-estates are, by their design, improving the functional diversity of amphibians, birds and mammals and ultimately ecosystem functioning” (Alexander *et al.*, 2019a). This has led to rather broad statements such as “we believe that eco-estates could provide an effective mitigation method of population expansion whilst maintaining ecosystem health but only under the recommended development and management plans” (Alexander *et al.*, 2019a). These studies further recommend that eco-estate development be focused on land which had previously been transformed, in particular agricultural and urban land (Alexander *et al.*, 2019c). While constructing eco-estates on previously transformed land is sensible approach given it negates the need to transform natural land, it does not necessarily reflect the true impact of eco-estates on native fauna. Furthermore, given research has focused on Kwa-Zulu Natal, which is characterized by a fundamentally different suite of species, further research on eco-estates in the Western Cape and elsewhere in South Africa is necessary (Alexander *et al.*, 2019a).

Hypotheses, aims and objectives

Eco-estates are a rapidly growing sector of the property market in South Africa (Alexander *et al.*, 2019a, 2019b; Mistry and Spocter, 2020) and globally (Reed, Hilty and Theobald, 2014). It is thus important to understand the “eco” component of “eco-estate” and the potential impacts of these developments on both wildlife and commensal species. In this dissertation I test the hypothesis that eco-estates do not adversely impact native wildlife and may allow wildlife communities to persist within a matrix of residential and recreational land use. The aim of this study is therefore to quantify differences in species composition across multiple taxa between a golfing eco-estate and the neighbouring natural land that is representative of the land before the estate was constructed. In addition, I compare avian species richness in this study with that of a previous study (Fox and Hockey 2007) when the estate was in the early phases of development (2005) providing a before and after comparison for this class of indicators.

Outline of dissertation

In **Chapter 2** I introduce the two study sites, Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR) and outline the general approach and methods I used to understand how a land use change from natural to a golf eco-estate may have impacted local fauna.

Chapters 3, 4 and 5 are data chapters in which I compare the small mammal (Chapter 3), medium-sized mammal (Chapter 4) and avian communities (Chapter 5) respectively, on both the estate and the reserve.

In **Chapter 6** I summarize my findings and discuss them with the broader framework of how land use influences biodiversity and whether the “eco” in eco-estate is a valid suffix or merely greenwashing.

CHAPTER 2: General Methods

Study area

This research took place on both the Atlantic Beach Estate (33°44’27”S, 18°26’56”E), and an adjacent nature reserve, Blaauwberg Nature Reserve (33°45’54”S, 18°27’09”E). These sites are approximately 25 km north of the City of Cape Town and fall within the Cape Town metropole (Figure 2.1).

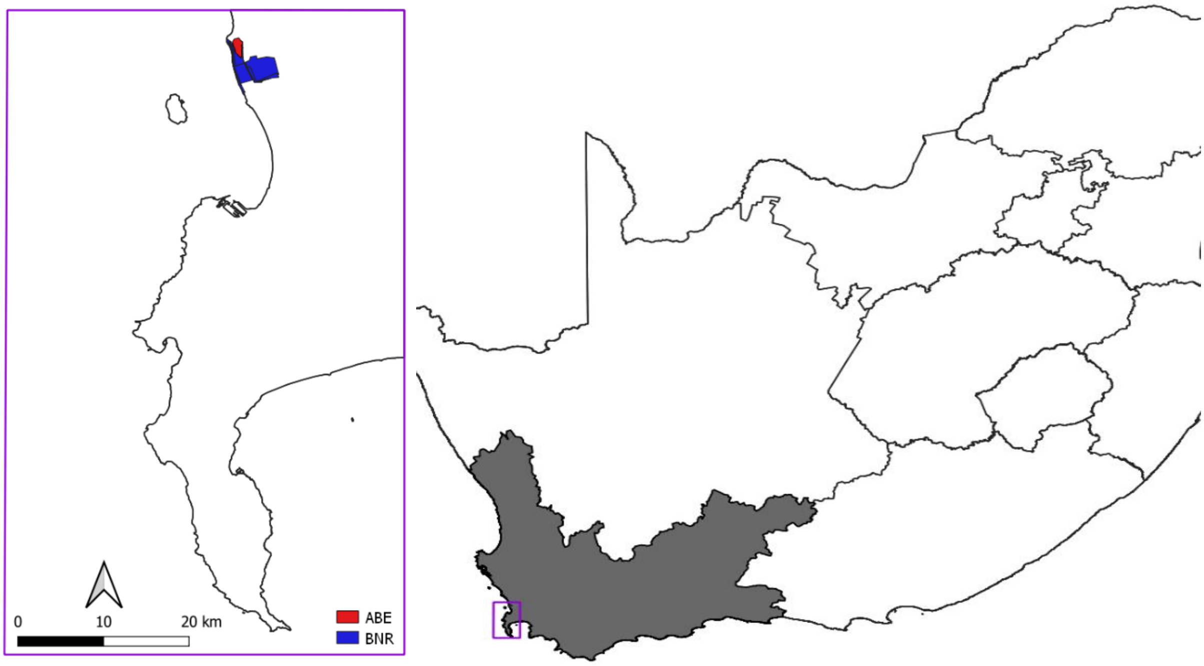


Figure 2.1: Atlantic Beach Estate and the Blaauwberg Nature Reserve are situated adjacent to one another approximately 25 kilometres north of the City of Cape Town, on South Africa’s West Coast.

Atlantic Beach Estate (ABE)

The estate is home to approximately 2300 residents and is adjacent to the small town of Melkbosstrand (which had a population of 11 500 people at last count, Statistics South Africa, 2011) and the coastal sector of the Blaauwberg Nature Reserve (Figure 2.2). The estate comprises 136 ha of residential land owned and managed by the Atlantic Beach Homeowners Association and 28 ha of golf estate and Cape Flats Dune Strandveld fragments owned by the City of Cape Town but managed by the Atlantic Beach Homeowners Association on a 50-year lease with an option to renew (van Wyk, 2017; P. Glanville, 2021, *pers. comm.*). The estate is approximately 2 kilometres in length (from north to south), and 0.5 kilometres wide (east to west) at its widest point.

The land on which the estate was established was cleaved off from what would become Blaauwberg Nature Reserve in 1995, when Johnnic and Grinaker were awarded a development contract (Rimbault, 2017). Construction began in 1997 in the northern half of the estate, with the first residents moving in by 1998. Construction in the northern half the current estate was completed in 2002. The property was then sold to Skeena Trading company (a consortium led by Rabie Group), who finished the development in 2005 (Rimbault, 2017). The estate has remained relatively structurally unchanged since development concluded.

The vegetation on the estate is a mosaic of indigenous and exotic species. Invasive Kikuyu grass (*Pennisetum clandestinum*) and a Cynodon turf grass hybrid (*C. dactylon* x *C. transvaalensis*) are used on the golf greens and fairways (Fox and Hockey, 2007). Trees and other exotic plant species can be found on the estate's list of permitted flora and as a result are widely distributed around the estate (Atlantic Beach Homeowners Association, 2017). In addition, a wide variety of both indigenous and alien plant species can be found in residents' gardens. The remnant patches of natural vegetation in the estate are characterised by Cape Flats Dune Strandveld (van Wyk, 2017).

Natural open spaces on the estate are heavily managed. The City of Cape Town has mandated the estate to remove invasive exotic vegetation in public open spaces although the level to which this is enforced is unclear (City of Cape Town, 2018). To maintain a functional golf course, the estate irrigates daily and employs ground staff to maintain the greens and fairways. The estate practices active fire suppression, preventing the continuation of natural processes associated with an appropriate fire regime (Ecosense, 2012). All snakes caught near residential houses are moved from residents' properties and placed in the nearest patch of natural vegetation outside of the estate. The estate has also introduced non-native animal species, such as springbok (*Antidorcas marsupialis*) which roam freely, are monitored and their numbers regulated through capture and translocation (van Wyk, 2017).

Figure 2.2: Aerial view of Atlantic Beach Estate, from the north. The vegetation bordering the reserve is within Blaauwberg Nature Reserve. Note Table Mountain, with the City of Cape Town surrounding its base, featuring prominently on the horizon (*Atlantic Beach Estate*, 2020).

The estate has approximately 860 residential houses, each of which is allowed two domestic cats (*Felis catus*) and two domestic dogs (*Canis lupus familiaris*) according to internal estate rules (Atlantic Beach Homeowners Association, 2013). While rules govern the number of pets per household, the total number of cats and dogs living on the estate is unclear (Nattrass and O'Riain, 2020). Estate regulations require domestic animals to be confined to the owner's property, or released conditionally on a leash, to avoid predation of small mammals, birds and reptiles both on the estate and in the surrounding nature reserve (Atlantic Beach Homeowners Association, 2013). However these rules are not strictly enforced and cats routinely roam beyond their owners properties (Nattrass and O'Riain, 2020).

A condition for the approval of the estate was that there would be a permeable fence between the estate and the reserve, allowing the free flow of animals between the reserve and the Dassenberg Coastal Catchment Partnership, north of Melkbosstrand (*Biodiversity agreement between the Western Cape Nature Conservation Board and the City of Cape Town*, 2018). The fence surrounding the estate is not, however, uniformly permeable to wildlife. The western fence, which borders the reserve consists of wire mesh with a 5 cm hole size, together with approximately 20 strands of electrified wire extending from the ground to 2.4 m in height. The top portion of the fence forms a 45^o anti-climb overhang of electrified strands on the outer side (facing the reserve). Thus the western fence is impenetrable to any animal larger than a rodent (Nattrass, 2019). The northern fence of the estate consists of a bar fence with electric wires, making the fence more permeable to larger mammals

(Nattrass, 2019). The adjacent suburb of Melkbosstrand to the north, minimizes the likelihood of animal movement through this section of the fence. That the fence is mostly impermeable, at least to larger mammals, is confirmed by van Wyk (2017) who comments that the fence represents a "significant barrier" to Cape grysbok (*Raphicerus melanotis*) dispersal out of the estate. However, the estate's boundary fence is not entirely impermeable to medium and large sized animals as caracal (*Caracal caracal*) have been witnessed on closed-circuit television entering and exiting the estate through a variety of routes, including over the fence and through gaps in the bar fencing at the main vehicle entrances to the estate (Appendix 2.1).

Blaauwberg Nature Reserve (BNR)

Blaauwberg Nature Reserve is situated on the West Coast of South Africa, 20 km north of Cape Town, but within the Cape Town metropole, on the outskirts of Bloubergstrand. The reserve comprises two sectors: the coastal sector located between the R27 and the coast, and the hill sector, located to the east of the R27 (Figure 2.3). What is now the reserve was proclaimed a conservation area in 1996 (Friends of BNR, 2017). The land is historically significant having played host to the Battle of Blaauwberg in 1806 and containing World War II defense outposts, in addition to Stone Age and Khoisan relics, leading to its protection under the National Monuments Act (Act 28 of 1969) (Küyler, 2011). The reserve itself was officially proclaimed in 2007 after recognizing the numerous endemic species that reside within its borders, and currently encompasses 1445 ha.

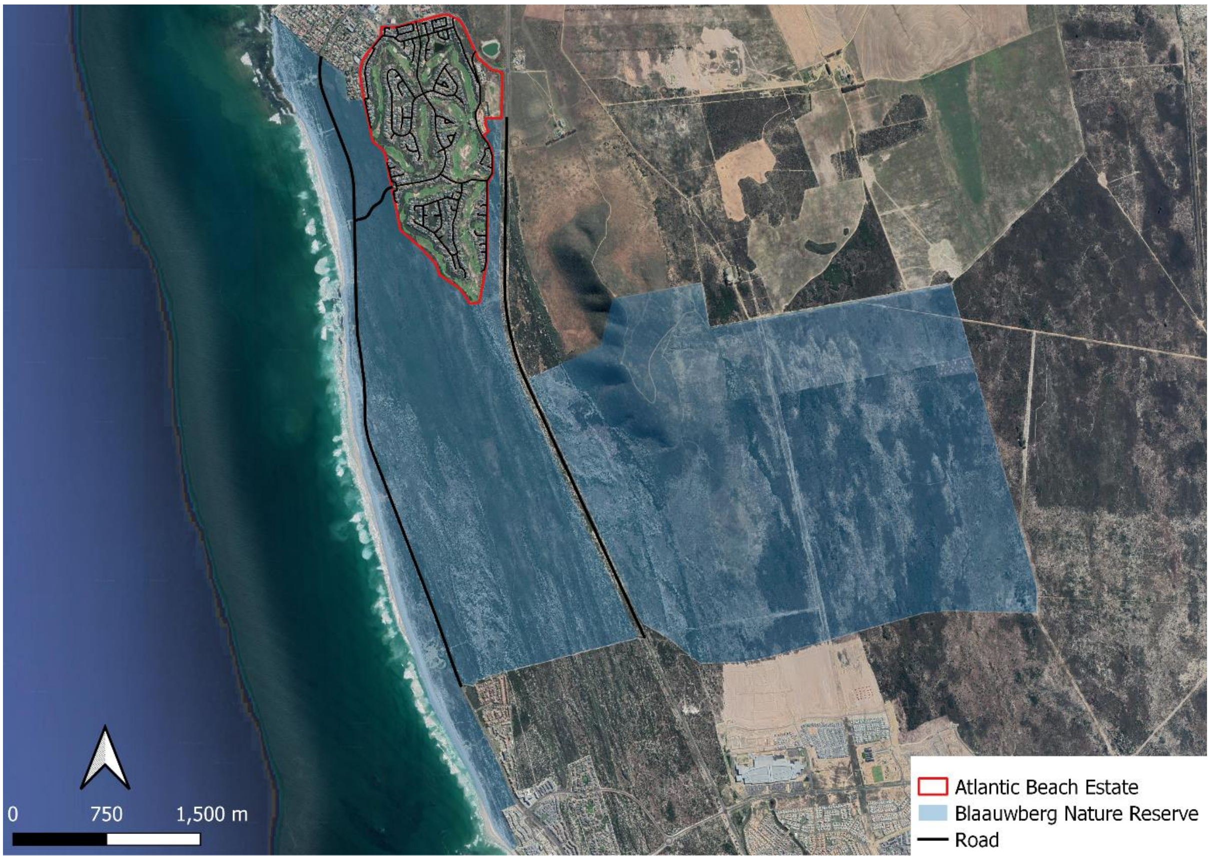


Figure 2.3: The extent and relative position of Blaauwberg Nature Reserve (light blue shading). Otto du Plessis Drive lies alongside the coast, while the R27 runs parallel to the coast, but further inland (both shown in black). The coastal sector of the reserve lies to the west of the R27, while the hill sector lies to the east. Atlantic Beach Estate (red outline) and the roads therein (black lines within the red outline) are also displayed.

The reserve falls within the Cape Floristic Region, one of six flora Kingdoms, characterised by exceptionally high levels of diversity and endemism (Goldblatt, 1978). In addition, the Cape Floristic Region is a biodiversity hotspot, which recognizes that the region not only has high levels of biodiversity, but is also threatened with extinction (Myers *et al.*, 2000). The reserve is home to three highly threatened vegetation types: Cape Flats Dune Strandveld, Swartland Shale Renosterveld and Cape Flats Sand Fynbos, which cumulatively include 559 plant species (Küyler, 2011). The coastal sector of the reserve is entirely Cape Flats Dune Strandveld, while the hill sector contains patches of all three vegetation types. The reserve supports numerous faunal species including four amphibian, 140 bird, 42 mammal (including whales, dolphins and seals) and 28 reptile species (Küyler, 2011). Eight of these faunal species have a threat status more severe than "least concern" on the IUCN Red List of Threatened Species.

The reserve is actively managed. Anthropogenic fires are quelled to prevent intrusion on to the neighbouring properties (Küyler, 2011). While the Blaauwberg Nature Reserve Integrated Reserve Management Plan recognizes the importance of fires in maintaining ecological integrity in the fynbos

(Küyler, 2011), active fire suppression and a lack of planned burns has led to vegetation thickening and many areas being overgrown (Fox and Hockey, 2007). Fire breaks have been maintained on the border between the reserve and the estate. Alien vegetation has invaded some parts of the reserve, though this vegetation is cleared in accordance with City of Cape Town policy (Biodiversity Management Branch, 2008). To date, primarily woody alien invasive species (such as *Acacia saligna* and *A. cyclops*) have been removed from the site (Küyler, 2011).

Justification for comparison and mirrored sampling approach

The estate and the coastal sector of the reserve are adjacent to one another and hence experience the same environmental conditions. The area has a Mediterranean climate characterised by warm, dry summers and cool, wet winters (Cowling, MacDonald and Simmons, 1996; Kottek *et al.*, 2006) with an annual average rainfall of 375 mm (Küyler, 2018). Both sites are situated in the vicinity of the Atlantic Ocean, which moderates the climate, preventing large temperature fluctuations. Both sites would naturally be characterised by Cape Flats Dune Strandveld, which still predominates in the coastal sector of the reserve and is the dominant vegetation type in the natural areas of the estate (Fox and Hockey, 2007). Theoretically, conditions on the estate before development closely resembled that found in the reserve. Therefore, the reserve can be seen as a control site for what was in the area, with the estate being the transformed or experimental unit.

I based all my data collection on a mirrored approach between the estate and the reserve, comparing the biodiversity on the estate with what one would expect should the estate not be there - in essence the reserve. I first defined sampling stations within the estate, then mirrored the placement of stations in the reserve to ensure equal effort and spacing between stations across both sites. In effect therefore I took the outline of the estate and superimposed it onto the reserve, accompanied by a slight rotation about its axis. The area selected represents the best example of undisturbed natural habitat within the reserve being furthest from roads (the R27 and Otto du Plessis Drive) and settlements (Bloubergstrand and the estate) and minimizing possible edge effects (Figure 2.4).

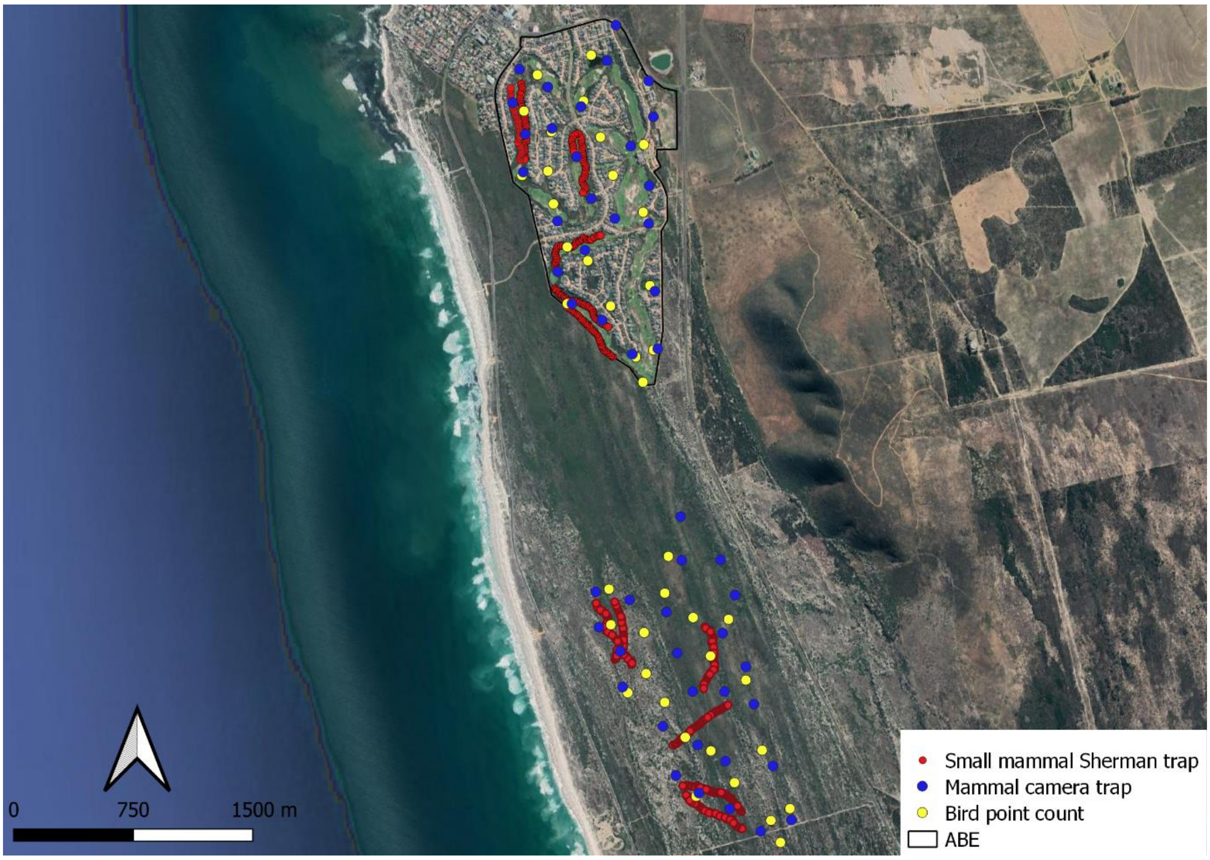


Figure 2.4: Relative positions of all small mammal Sherman traps, mammal camera traps and bird point counts across Atlantic Beach Estate (cluster to the north) and Blaauwberg Nature Reserve (cluster to the south).

Within the estate I sampled primarily in the remnant Strandveld but also on the golf course and in the golf course buffer area (the five meters around the edge of the course; specific details to follow in relevant chapters). I recognize that residential gardens generally comprise the bulk of residential land (Goddard, Dougill and Benton, 2010; van Heezik, Dickinson and Freeman, 2012) and have the potential to support numerous native species and provide essential ecosystem services (Aronson *et al.*, 2017; Shackleton *et al.*, 2018; Soanes and Lentini, 2019; Soanes *et al.*, 2019; Gonçalves *et al.*, 2021; Larson *et al.*, 2022). I argue that the estate has a slightly different configuration to a typical residential area as residential gardens on the estate are generally small, primarily grass-covered and fenced in, limiting movement of medium-large mammals between adjacent plots and containing domestic animals which present severe hazards to native wildlife (Young *et al.*, 2011; Hughes and Macdonald, 2013; Seymour *et al.*, 2020). On this estate, residential gardens contain some private features (e.g., pool, trampoline, favourite plants), but the estate as a whole serves as a larger, communal "garden". I therefore did not sample directly in residential gardens. However, numerous sampling stations were located on the periphery of residential gardens, allowing birds in particular to be sampled even when perched within residential gardens. Medium sized mammals routinely utilize residential gardens (Baker and Harris, 2007; Van Helden, Close and Steven, 2020), but I argue that they are unlikely to fully complete their life cycle within the confines of a residential garden on the estate, resulting in these species having to leave the residential garden, onto the broader estate and hence having a non-zero detection probability at sampling stations. Small mammals could persist entirely within residential gardens, however their abundance may be limited by predation and distance to nearest natural vegetation (Baker *et al.*, 2003). The small residential gardens consist primarily of natural vegetation and grass and should therefore be somewhat similar to conditions just outside the garden.

Statistical analyses and mapping

Unless otherwise mentioned, all statistical analyses were performed within R version 3.5.3 (R Core Development Team, 2020) through the R Studio interface, version 1.1.456 (RStudio Team, 2016). I frequently utilized the tidyverse for data manipulations and for plotting data (Wickham *et al.*, 2019; Wickham, 2021). I performed all geographic information system (GIS) mapping in QGIS Zanzibar version 3.8.0 (QGIS Development Team, 2016).

I designated land within the confines of Atlantic Beach Estate into residential area, golf course and natural land, using the City of Cape Town's Biodiversity Network GIS layer (available at https://web1.capetown.gov.za/web1/OpenDataPortal/DatasetDetail?DatasetName=Biodiversity%20 network). The Biodiversity Network has classified non-urban land within the City of Cape Town metropole into 12 different classes. Within the estate, I consider all patches which have been deemed "irreversibly modified site of conservation significance" within the Biodiversity Network as "golf course." Similarly, the Biodiversity Network designated some patches within the ABE as "connectivity site," "remnant strandveld," "unselected natural area of conservation significance" or "unselected natural area: good/fair/restorable" which I collectively define as "natural areas." I classified all remaining areas within the estate as "residential." This includes residential houses and gardens, as well as the road network within the estate. The city officials have left these areas unassigned in the Biodiversity Network GIS layer. I manually added additional features not included in the layer but visible on a Google Maps plugin in QGIS. All land within the reserve was considered "critically endangered vegetation of low/restorable condition" by the Biodiversity Network.

Notes on terminology

Throughout this thesis, I distinguish between terrestrial small mammals and all other terrestrial, non-volant mammals. The term "small mammals" refers to all terrestrial mammals < 500 g, while "mammals" refers to any terrestrial mammal > 500 g. This distinction is a practical one, based on the sampling methods available, with small mammals able to be captured using commercial live traps and are not reliably detected by camera traps, while images of medium-large mammals were captured on camera traps (Hoffman *et al.*, 2010). I did not specifically sample for moles and molerats, though they are occasionally captured in Sherman traps and are thought to occur in the area (G. Bronner, 2019, *pers. comm*.)

Appendix 2.1 Caracal scaling an electric fence

Figure S2.1.1: Security camera footage showing a caracal scaling the electric fence surrounding Atlantic Beach Estate.

CHAPTER 3: Small Mammals

Abstract

Small mammals are a diverse taxon, occupying many different niches and performing a multitude of different functions across a range of ecosystems. Their ease of capture, widespread distribution and rapid response to environmental changes, explains their importance as an indicator taxon for anthropogenic impacts. Here I compared the small mammal communities on Atlantic Beach Estate, a high security eco-estate near Melkbosstrand, and the neighbouring Blaauwberg Nature Reserve. I established a total of 12 lines of 50 traps set 10 m apart, divided equally between the two sites and sampled for six consecutive nights in October 2019. There were more captures on the reserve (432 compared to 273), with 60 % of estate captures comprised of the four-striped grass mouse, *Rhabdomys pumilio*. Species richness was the same for both sites (n=12) but was more even and more diverse on the estate, with a higher Shannon-Wiener diversity (1.69 versus 1.43 for the estate versus the reserve respectively), Pielou's evenness (0.68 versus 0.58) and Brillouin Index (1.61 versus 1.37) though a lower Simpsons Index (0.58 versus 0.75). Both sites had three unique species and in general trap lines were more similar within than between sites. Both sites had the same species richness, and both were dominated by early pioneer species (*R. pumilio* and *Mus munitoides*). The estate had an introduced species, the house rat (*Rattus rattus*), though localized and in small numbers, while the reserve had a threatened species, the white-tailed mouse (*Mystromys albicaudatus*). The estate maintained a diverse array of small mammal species, though without habitat specialists. Species composition was mediated by the distance to the edge of the estate, with a more "natural" composition found along the boundary between the estate and the nature reserve.

Introduction

Small mammals are a diverse taxon, occupying many different niches and performing a multitude of different functions across a range of ecosystems. Their cosmopolitan distribution, small size and sheer abundance means they are central to the diets of many other species including reptiles, birds and mammalian carnivores (Amar *et al.*, 2018; Leighton *et al.*, 2020). In certain systems vegetation is regulated from the top-down by small mammals (Weltzin, Archer and Heitschmidt, 1997). Small mammals commonly eat seeds, and this granivory (seed predation) is postulated to have driven the evolution of various adaptations by plants. Serotiny (the retention of seeds in a pod or cone until after a fire), myrmecochory (seed dispersal by ants), other seed dispersal mechanisms (e.g., wind dispersal) and other pollination syndromes all decrease the chances of seeds being consumed by small mammals (Janzen, 1971; Weltzin, Archer and Heitschmidt, 1997). Some plant species have adapted to utilise small mammals instead of avoiding them through scatter hoarding, whereby produce seeds which are attractive to small mammals who collect the seeds and bury them elsewhere, facilitating the dispersal of numerous plant species (White, Bronner and Midgley, 2017). Small mammals are also important pollinators, particularly in certain areas such as the Cape Floristic Region (CFR) (Wiens *et al.*, 1983; Zoeller *et al.*, 2016). Additionally, and particularly in the CFR, fossorial small mammals may be important in promoting the establishment of fynbos seedlings (Holmes, 2008). In general, the presence of a rich, diverse small mammal community indicates the potential to fulfill a huge assortment of roles with an ecosystem, while the lack thereof leaves the ecosystem missing a critical component.

Small mammal communities are shaped primarily by bottom up forces as opposed to being regulated by top down control (Kerley, 1992). These bottom up forces may occur at a patch or a landscape scale, and include habitat complexity and heterogeneity (Powell, Belitsky and Rathbun, 1981; Els and Kerley, 1996), density and complexity of understory vegetation (Shanker, 2001), fire (Fox, 1990), proximity to water (Bond, Ferguson and Forsyth, 1980), landscape context and isolation (Kozakiewicz, 1993), diversity and availability of food resources (Meserve, Milstead and Gutiérrez, 2001) and the available productivity of a habitat. Changes to bottom up forces can dramatically alter species composition, depending on which species are better suited to the new habitat conditions (e.g., Rebelo, Rebelo, Rebelo, & Bronner (2019)). While bottom up forces are a key driver of small mammal communities, top down and parallel processes are important, primarily through predation and inter-specific competition (Korpimäki and Krebs, 1996).

A peri-urban landscape presents a unique blend of challenges for small mammals, with both bottom-up and top-down forces all playing out within a novel landscape (Pickett *et al.*, 2001; Hobbs *et al.*, 2006; Kowarik, 2011). Compared to natural habitats, peri-urban landscapes introduce supplementary food and water (e.g., waste, irrigation, fertilized lawns), offer protection from certain predators (e.g., caracal (*Caracal caracal*)), add novel predators (e.g., domestic cats (*Felis catus*)) (Crooks and Soulè, 1999), create new habitats (e.g., dams, parks), reduce existing natural habitat and are subject to sensory pollution in the form of noise and light (Longcore and Rich, 2004; Francis, Ortega and Cruz, 2009). These conditions have the potential to alter the abundance, richness and composition of small mammal communities depending on the relative influence of each of the new forces. Excess urbanization without appropriate attention to important landscape features for small mammals results in decreased diversity and abundance of small mammals, and a shift in composition, where specialist species are replaced by generalists, which are often introduced species (e.g., house rat (*Rattus rattus*)) (Fernández and Simonetti, 2013; Klimant *et al.*, 2017). Small mammal community composition varies greatly across peri-urban areas and is governed by the degree to which peri-urban areas maintain natural features as well as structural complexity, heterogeneity and connectivity (Garden, McAlpine and Possingham, 2010; Fischer, Thies and Tscharntke, 2011).

Most small mammals are relatively short-lived, their numbers closely track changes in environmental conditions and their cosmopolitan distribution means they can be studied almost anywhere (Barnett and Dutton, 1995). Together these factors make them good bio-indicators, particularly for assessing anthropogenic impacts (e.g., Joubert and Ryan, 1999; Avenant, 2000). The rapid population turnover of small mammals closely tracks changes in the environment with only a short lag period. In addition to monitoring total species abundance, changes in relative species abundance, species diversity and evenness can provide insights into how environmental changes impact different species. Other traits which make small mammals suitable as indicator species include their relative ease of identification and that they can be sampled relatively inexpensively and with minimal harm to the animals involved (Avenant, 2011) or risk to those handling the animals (Barnett and Dutton, 1995).

Many aspects of organismal biology are influenced by body size and this is most pronounced in small mammals, which “live fast and die young” (Sibly and Brown, 2007). There are various eco-physiological correlates of mammal body size which are related to allometric scaling (i.e., how bodily characteristics change with size) (Schmidt-Nielsen, 1975). Longevity and vagility scale positively with body size and hence small mammals are generally shorter lived and less able to move about their environment than their larger counterparts (Speakman, 2005). In contrast, metabolic rates scale negatively with body size hence smaller mammals have a higher net energy demand and therefore depend on energy-rich foods, such as seeds, pollen, succulent foliage and insects, which in turn leads to greater competition and niche packing (Speakman, 2005). Litter sizes, intervals between litters and maturation times scale negatively with increasing body size. Small mammals exhibit a short timeframe between birth, reproduction and death and thus have a rapid intergenerational turnover. These factors together mean that as a collective, small mammals respond quickly to environmental changes with numbers rising and falling closely with changing environmental conditions (Avenant, 2011).

Hypothesis and predictions

Given the varied responses of small mammal species to human modified land, the importance of small mammals to environmental health, particularly within the CFR, and the increasing frequency of eco-estates in South Africa, investigating the effects of eco-estates on small mammal communities is crucial. I hypothesized that land use would affect the diversity and abundance of small mammals and predicted that diversity would be lower on the estate but that select generalist, pioneer species (e.g., the four-striped grass mouse (*Rhabdomys pumilio*) and the pygmy mouse (*Mus minutoides*)) would have higher relative abundance on the estate compared to the reserve. I also predicted that specialist and/or rare species would be more likely to be detected in the reserve than on the estate because of loss of natural habitat and essential ecosystem level processes in the latter (Lagesse and Thondhlana, 2016).

Methods

Data collection

Arranging traps in a grid allows for both density and home range size estimation (Barnett and Dutton, 1995). However, in a fragmented environment such as the estate habitat patches were too small effectively restricting me to the use of line transects, following Hoffman *et al.* (2010). Each transect was approximately 490 m long with traps (n=50) placed approximately 10 m apart. I placed traps in the most suitable piece of local habitat, within a one meter radius of each trap station to maximize trapping success, following a series of well-established principles for small mammal trapping including: placement under shelter, flush with the ground to allow the animal to walk straight into the trap and near discernable rodent paths (Barnett and Dutton, 1995; Hoffman *et al.*, 2010). I recorded the global positioning system (GPS) positions of individual traps to facilitate trap/capture recoveries especially in dense vegetation. All Sherman traps were cleaned before and after use to prevent the spread of pathogens from prior trapping sessions and to avoid potential biases linked to odours of previously captured individuals (Heske, 1987). I sampled small mammal populations using Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida), within both the estate and the reserve during September 2019. Sherman traps are effective in catching many small (< 500 g), terrestrial mammals, however this method generally precludes fossorial and volant mammals (such as moles, molerats and bats) G. Bronner, 2019, *pers. comm.*).

In the estate, I set six trap lines in remnant patches of Strandveld (Figure 3.1; Appendix 3.1). I placed two pairs (n=4) of trap lines in patches of natural vegetation which were at least 500 m long but separated by golf course fairways (approximately 50 m wide). Small mammal abundance is low on golf fairways which lack any structural complexity (Hodgkison, Hero and Warnken, 2007) and thus these paired transects were considered to be independent. The remaining two trap lines were unpaired and were located within suitably sized continuous patches of natural vegetation. The irregular spatial configuration of trap lines in the estate was a result of the fragmented natural habitat, and the importance of placing traps within natural habitat, as Strandveld vegetation is dense and thus I placed traps in vegetation just off the edge of footpaths, and along the edge of the golf course to enable access for repeat sampling of traps.

I did not place traps in residential gardens. Trap lines were placed on the periphery of residential gardens, which would allow for movement from residential gardens to the traps. I argue that in this case, residential gardens are small, predominantly grass covered, routinely contain domestic animals, and lack the structural complexity of natural patches just outside the gardens. The natural patches selected therefore represent the best habitat for small mammals within the estate.

I mirrored the trap lines configurations established on the estate in the reserve to control for effort and trap spacing between trap lines. I set six trap lines (each with 50 traps) along transects that penetrated deep into the nature reserve, where there was sufficient natural habitat far from nearby roadways and buildings, thus minimizing possible disturbance effects (Figure 3.1; Appendix 3.1).

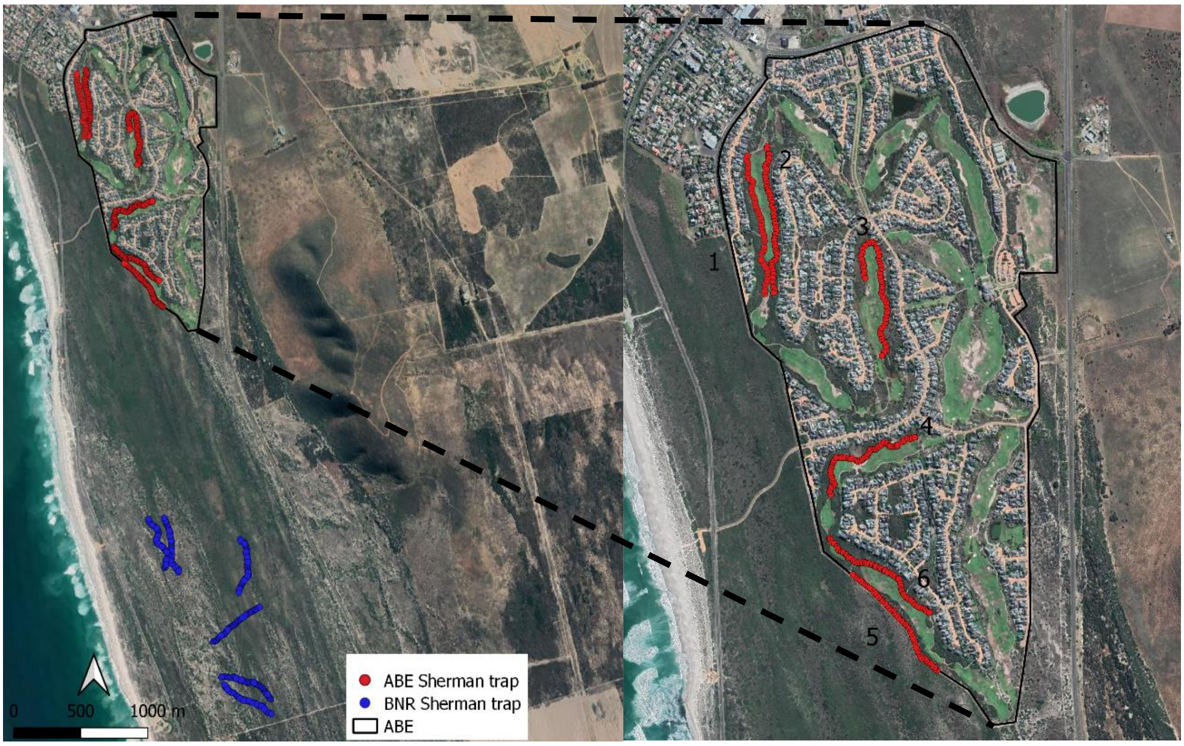


Figure 3.1: Position of small mammal trap lines on Atlantic Beach Estate (ABE, red dots) and Blauuwberg Nature Reserve (BNR, blue dots). The insert (right) shows a magnified view of the trap line configuration on ABE, with each trap line numbered. The start and end locations of each trap line can be found in Appendix 3.1.

I conducted trapping over two sessions. In each session I simultaneously had three trap lines open in the estate and three trap lines open in the reserve (Table 3.2). After the first session I moved all the traps to new locations to start the second session (Table 3.2). This approach ensured that differences in species abundance and observed community composition were independent of local weather effects that may affect trapping success (Sidorowicz, 1960; Gentry, Golley and McGinnis, 1966). In total I had 12 trap lines of 50 traps, each of which was operational for six nights, resulting in 300 traps open each night for 12 nights for a total of 1800 trap-nights per site (excluding trap failures).

Table 3.2: Summary of trapping effort on Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR).

Site	Trapping session	Trap line	Start date	End date	Calendar nights
ABE	1	4, 5, 6	13 October 2019	18 October 2019	6
BNR	1	10, 11, 12	13 October 2019	18 October 2019	6
ABE	2	1, 2, 3	19 October 2019	24 October 2019	6
BNR	2	7, 8, 9	19 October 2019	24 October 2019	6

I took various precautions to minimize stress on the animals and increase the probability of capture including trapping exclusively at night to minimize trap mortalities associated with high diurnal temperatures. Each evening I set the traps (placed whenever possible under cover such as vegetation, rocks or logs (Tasker and Dickman, 2002)) in the two hours before dusk (17:00 to 19:00) and checked each trap in the morning within four hours after dawn (6:20 to 10:00). Each trap was covered by an aerothane foam sheet providing insulation and thus minimizing temperature extremes. Bait selection is an important consideration when conducting small mammal trapping and influences trapping success (Willan, 1986). I used a standard mixture of peanut butter, sunflower oil, rolled oats, Bovril, Chick Chick (ground maize) and raisins as bait (Patric, 1970), supplemented with a small piece of fruit (de-pipped apple or rehydrated raisin) as a source of moisture for captured animals (Barnett and Dutton, 1995).

Small mammals were processed at the site of capture following Hoffman *et al.* (2010). Each animal was transferred from the trap into a plastic mesh bag, identified to species level, weighed (to the nearest gram using a 200 g limit Salter spring balance (Salter, Perth, Western Australia)) and sexed. Species were identified using a preliminary checklist of the terrestrial small mammal species that may occur at the estate and surrounding portions of nature reserve (within the QDS 3318CD) and was based on ~460 000 mammal point distribution records compiled by the Endangered Wildlife Trust for the 2016 Mammals Red List (Child *et al.*, 2016). Literature and museum database records were sorted by geographic co-ordinates for the Orders Eulipotyphla, Rodentia, Afrosoricida and Macroscelidea, and then screened (based on habitat preferences and availability) by Dr. Gary Bronner (Co-Supervisor). Although the “first glance” identification guide (see Appendix 3.2) may seem very superficial, it is based on robust distribution data for a subset of species that are relatively easy to distinguish, and the few morphological characteristics that are given to distinguish between species are the best traits for field identification. I also consulted a more detailed field guide (Stuart and Stuart, 2015) to assist with field identifications. Small mammals were sexed on the basis of their anal-genital distance, the distance between the base of the penis or vaginal opening and the anus, with males having a larger distance than females (Hoffman *et al.*, 2010). Each individual was marked in two positions, one in a "base" position and one in a "secondary" position, to facilitate later identification (Figure 3.2). Initially I used fur-clipping as the base mark, however within two nights it became apparent that this was difficult to spot on recaptured individuals. We therefore switched to using a paint marker in both the base and the secondary mark. Processing time was two to three minutes per animal and recaptured individuals were released as soon as they had been checked for markings.

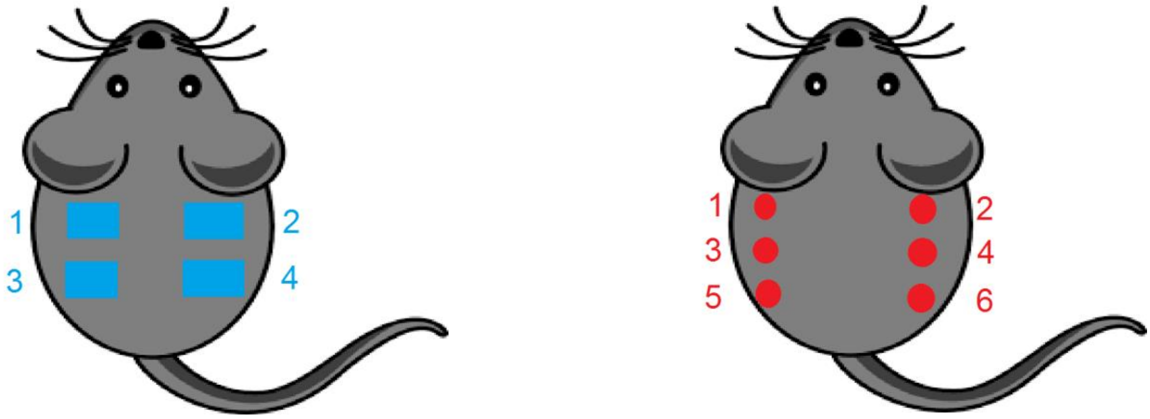


Figure 3.2: Fur clipping/paint marker spot positioning ("base mark") (left) and paint marker positioning ("secondary mark") (right).

The abovementioned trapping protocol (including traps and bait) is standard for surveying purposes both in South Africa and abroad, and many studies have shown that this procedure has no noticeable effect on the survival or ecology of the captured small mammals (Hoffman *et al.*, 2010; Sikes and Gannon, 2011; Bosson, Islam and Boonstra, 2012). This study was granted ethical approval by the University of Cape Town Science Faculty Animal Ethics Committee (reference number: 2019/v15/JOR) and was sanctioned by the Atlantic Beach Estate Homeowners Association, with permits obtained from CapeNature (reference number: CN44-28-14525) and the City of Cape Town.

Data analyses

Given the short duration of survey trapping, I assumed that small mammal populations were closed with minimal birth/death and emigration/immigration (Kendall, 1999; Pacheco *et al.*, 2013). Although there are various probabilistic models for statistically estimating population sizes based on capture-recapture data, they almost invariably have inherent assumptions that are seldom satisfied under field conditions. Consequently, I used the direct enumeration method, whereby the minimum number of individuals per species (excluding recaptures) was used as an index of population size (Bronner and Meester, 1987). Although this method likely underestimates actual population sizes, enumeration estimates are usually concordant with probabilistic estimation results and are thus fairly robust

(Pacheco *et al.*, 2013), except when there are marked differences in species catchability (Kendall, 1999).

I visualized how species were distributed amongst the trap lines using the *plotweb* function in the R package *bipartite* (Dormann *et al.*, 2020). I constructed rank abundance curves for the estate and the reserve independently using the *radfit* function in the *vegan* package (Oksanen *et al.*, 2019). This function allows one to plot log species abundance against rank order (Whittaker, 1965) and then fits five potential models to explain the underlying pattern namely null, preemption, log-Normal, Zipf or Zipf-Mandelbrot (Wilson, 1991). The package then selects the best fitting model on the basis of Akaike's Information Criterion (AIC) (Bozdogan, 1987). The plots were visualized using the *lattice* package in R (Wright, 2020).

Unequal catchability of species is the norm in wildlife studies (Carothers, 1973). To assess catchability of species, I considered both inter- and intra-species variation in capture success. Inter-species catchability was assessed by plotting the total number of independent captures of each species across both sites against the total number of recaptures for each species across both sites, for all species which had at least one recapture. To assess intra-species catchability, I plotted the number of independent captures and the number of recaptures of a single species on one site, against the number of independent captures and the number of recaptures of the same species on the other site. I did this for all five species which had at least one recapture on both sites (four-striped grass mouse, pygmy mouse, vlei rat (*Otomys irroratus*), forest shrew (*Myosorex varius*) and Krebs's fat mouse (*Steatomys krebsii*)).

Data were screened for normality using Shapiro-Wilks tests within the *shapiro.test* function and by visually checking qqplots, both within the *stats* package in base R. If data were normally distributed, I tested for differences between means using a Welch Two Sample t-test. In cases where data were not normally distributed, I utilized Mann-Whitney U tests within the *wilcox.exact* function in the R package *exactRankTests* (Mann and Whitney, 1947; Hothorn and Hornik, 2019). In all cases I used a p-value<0.05 to indicate significance. I performed rarefaction analyses using the *rarefy* function in the R package *vegan* (Oksanen *et al.*, 2019) to assess whether sampling effort was sufficient. I performed individual-based (i.e., minimum sample size) rarefaction when comparing rates of species accumulation. This quantifies the number of trapped individuals required to reach an asymptote, as opposed to the number of trap nights necessary.

Three measures are regularly used to quantify and compare communities: species richness, diversity and evenness (Table 3.3). Species richness is the total number of species present at a particular site. Evenness is a measure of how the number of individuals are divided among the number of species

(Hill, 1973). Diversity incorporates both species richness and evenness, in essence calculating how well the number of individuals are split amongst the number of species, while also considering how many species are present. Evenness is scaled between 0 and 1, where 0 is the least even. Diversity index interpretation depends on the index – the Simpson diversity index is interpreted in the same way as evenness, where it is scaled between 0 and 1, with values close to 1 representing high diversity (Magurran, 2004). Shannon-Wiener and Brillouin indices are similar in their interpretation, with higher values representing communities which are more diverse. I calculated all diversity and evenness measures (Shannon-Wiener and Simpson diversity indices, Pielou's evenness and the Brillouin index) separately, for each site, so that I could contrast the values. The Shannon-Wiener diversity index and Pielou's evenness are robust to unequal sample sizes as was the case between the estate and the reserve. I included the Brillouin index, despite lower discriminatory power, as it accounts for potential unequal catchability between small mammal species (Magurran, 2004). The Simpson diversity index may be thought of as a dominance index, as it doesn't consider species richness, and therefore upweights dominant species (Simpson, 1949). I calculated Shannon-Wiener and Simpson diversity indices using the *diversity* function in the R package *vegan* (Oksanen *et al.*, 2019). Pielou's evenness is defined as the Shannon-Wiener diversity divided by the log of the total number of species. I created a function within R to calculate the Brillouin index.

Table 3.3: Evenness and diversity indices, with associated formula for index calculation, and variables involved in calculating the index (Magurran, 2004).

Index	Formula	Variables
Pielou's evenness	$J' = \frac{H'}{Hmax}$	$Hmax$ = maximum possible diversity
Shannon-Wiener diversity index	$H' = -\sum p_{\mathrm{i}} ln p_{\mathrm{i}}$	p_{i} = proportion of individuals in the $_{\mathrm{i}}th$ species
Brillouin index	$HB = \frac{lnN! - \sum ln n_{\mathrm{i}}!}{N}$	n = total number of organisms of a particular species N = total number of organisms of all species
Simpson diversity index	$D = \sum p_{\mathrm{i}}^2$	

I calculated the estimated species richness of each trap line, as well as the species richness of the estate and the reserve. I used the *ChaoSpecies* function in the R package *SpadeR* (Chao, Ma and Hsieh, 2015), with abundance data. This calculation was based on the number of unique captures of each species at each trap line, or of each species at each site. I utilized the iChao 1 output (Chiu *et al.*, 2014), which is an improved estimate of the original Chao (1984) estimate (Chao, 1984, 1987). Chao is a non-parametric estimate of true species richness, using the number of singletons and doubletons to estimate the species richness (Chao, 1984). The assumption is that the more singletons and/or doubletons of a species (i.e., the number of species caught only once or twice), the more likely it is that sampling failed to capture additional species. iChao 1 (2014) extends this by incorporating the number of tripletons and quadrupletons into species richness estimation. I also calculated the trap efficiency/effectiveness for each trap line, and for each site, by dividing the observed species richness by the iChao1 predicted species richness. I compared the estimated species richness with the effective number of species (or Hill number) - that is the number of equally abundant species needed to obtain the same mean proportional species abundance (Tuomisto, 2010). The effective number of species is increasingly being used, as it presents a potentially more accurate measure of species richness (Chao, Chiu and Jost, 2014). The effective number of species is computed as:

$$e^H$$

Where H is the Shannon-Wiener diversity index.

Diversity as a term is somewhat loose and can refer to several different scales. I quantified alpha, beta and gamma diversity where alpha diversity refers to the within trap line diversity, beta diversity refers to the diversity between trap lines, and gamma diversity refers to the site level diversity (Whittaker, 1972). I calculated beta diversity, or how diverse each trap line was relative to the other trap lines, by dividing the gamma diversity by the alpha diversity. In addition, I considered proportional species turnover using the following formula:

$$1 - \frac{alpha}{gamma}$$

I performed various comparisons between trap lines to assess the level of similarity between trap lines. I created a Sorensen pairwise similarity matrix using the *SimilarityMult* function in the R package *SpadeR* (Chao, Ma and Hsieh, 2015). This function contrasts the number of unique captures of each species at a trap line, against the number of unique captures of species at other trap lines to output a matrix of similarity. Trap lines which are more similar have values closer to 1.

I performed multiple other, visual measures of similarity to assess which trap lines more closely resembled one another. Like the Sorensen pairwise similarity, I compared the number of unique captures of each species at each trap line to the number of unique individuals of each species at every other trap line. I created a dissimilarity matrix of trap lines by first scaling a matrix of the number of unique captures of each species per trap line. I then computed a Pearson-based distance matrix between rows in the dataset using the *dist* function in the R package *factoextra* (Kassambara and Mundt, 2020). I visualized the output in the same package.

Results

A total of 3286 trap nights (after correcting for trap failures), resulted in 705 captures of 612 individuals (trap success of 21.5 % and a recapture rate of 15.2 %), representing 15 species (Table 3.4) or 65.2 % of rodent and shrew species thought to occur in the region (Avery, Rautenbach and Randall, 1990). The 1606 trap nights on the estate (194 trap failures), yielded 273 captures of 246 individuals (trap success of 17.00% and a recapture rate of 9.9 %), representing 12 species. The 1680 trap nights on the reserve (120 trap failures) yielded 432 captures of 366 individuals (trap success of 25.7 % and a recapture rate of 15.3 %), representing 12 species. The most frequently captured species on the estate was the pygmy mouse (*M. minutoides*) (n=115; minimum number alive (MNA)=102), while on the reserve it was the four-striped grass mouse (*R. pumilio*) (n=262; MNA=229). Each site had three unique species, with grey climbing mouse (*Dendromus melanotis*), house rat and reddish-grey musk shrew (*Crocidura cyanea*) found only on the estate and lesser dwarf shrew (*Suncus varilla*), Namaqua rock mouse (*Micaelamys namaquensis*) and white-tailed rat (*Mystromys albicaudatus*) found only on the reserve.

Table 3.4: The number of captures and minimum number alive (MNA) for each species trapped on Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR) respectively.

Species	**ABE**		**BNR**	
	Captures	**MNA**	**Captures**	**MNA**
Pygmy mouse (*Mus minutoides*)	115	102	34	26
Four-striped grass mouse (*Rhabdomys pumilio*)	58	54	262	229
Krebs's fat mouse (*Steatomys krebsii*)	41	36	15	14
House rat (*Rattus rattus*)[1,4]	21	20	0	0
Forest shrew (*Myosorex varius*)	14	13	18	16
Vlei rat (*Otomys irroratus*)	10	8	25	20
Hairy-footed gerbil (*Gerbillurus paeba*)	5	4	16	11
Cape gerbil (*Tatera afra*)	4	4	39	31
Brant's climbing mouse (*Dendromus mesomelas*)	2	2	1	1
Grey climbing mouse (*Dendromus melanotis*)[1]	1	1	0	0
Karoo bush rat (*Otomys unisulcatus*)	1	1	10	7
Reddish-grey musk shrew (*Crocidura cyanea*)[1]	1	1	0	0
Lesser dwarf shrew (*Suncus varilla*)[2]	0	0	1	1
Namaqua rock mouse (*Micaelamys namaquensis*)[2]	0	0	1	1
White-tailed rat (*Mystromys albicaudatus*)[2,3]	0	0	10	9
Totals	**273**	**246**	**432**	**366**

[1] Species unique to ABE.

[2] Species unique to BNR.

[3] The white-tailed rat is classified as "vulnerable" on the IUCN Red List of Threatened Species.

[4] Non-native.

Rarefaction curves for the estate and the reserve had not yet reached an asymptote, suggesting more sampling may have resulting in capturing additional species (Figure 3.3).

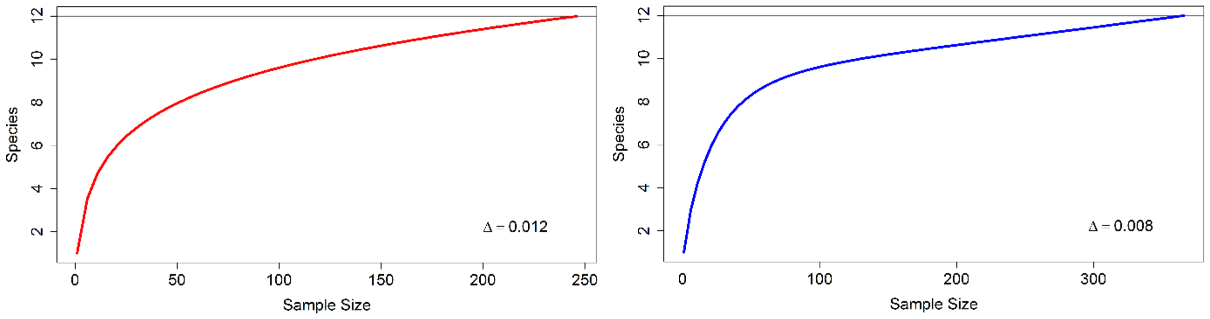


Figure 3.3: Rarefaction curve for Atlantic Beach Estate (left) and Blaauwberg Nature Reserve (right). The delta value represents the slope of the curve at the second to last sampling occasion.

Species rank abundance curves on the estate followed a pre-emption model, while on the reserve, they followed a Zipf model (Figure 3.4). Pygmy mice were the highest ranked species on the estate, while four-striped grass mice were the highest ranked species on the reserve.

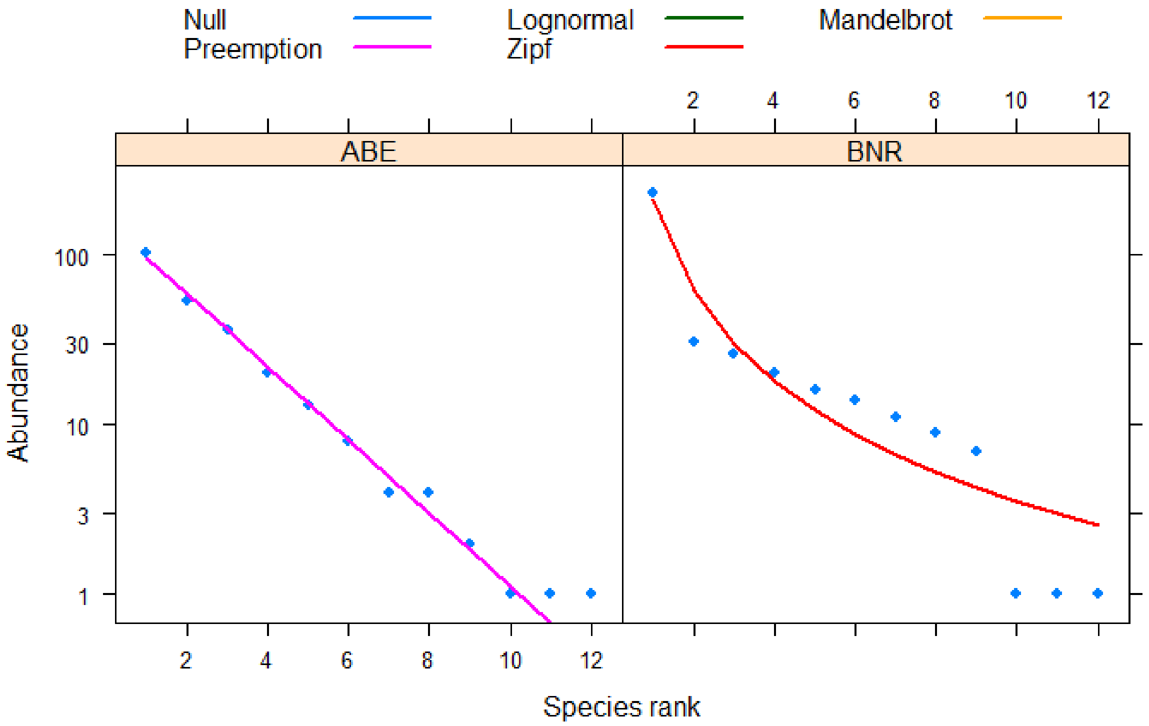


Figure 3.4: Species rank abundance models for Atlantic Beach Estate (left) and Blaauwberg Nature Reserve (right). Line colours represent the best fitting model for species rank abundance. Note that the y-axis (abundance) does not increase linearly but resembles a log increase.

Distribution amongst trap lines

Both the estate and the reserve had the same number of maximum captures on a trap line (n=91 for trap line 4 on the estate and trap line 7 on the reserve), but, in general trap lines on the reserve had more captures (Figure 3.5). Four-striped grass mice, the most captured species, were found on all trap lines, but predominantly on trap lines in the reserve, and particularly in trap lines 7 and 11. Pygmy mice were similarly captured on all trap lines, but were captured more frequently on estate trap lines, especially trap line 4.

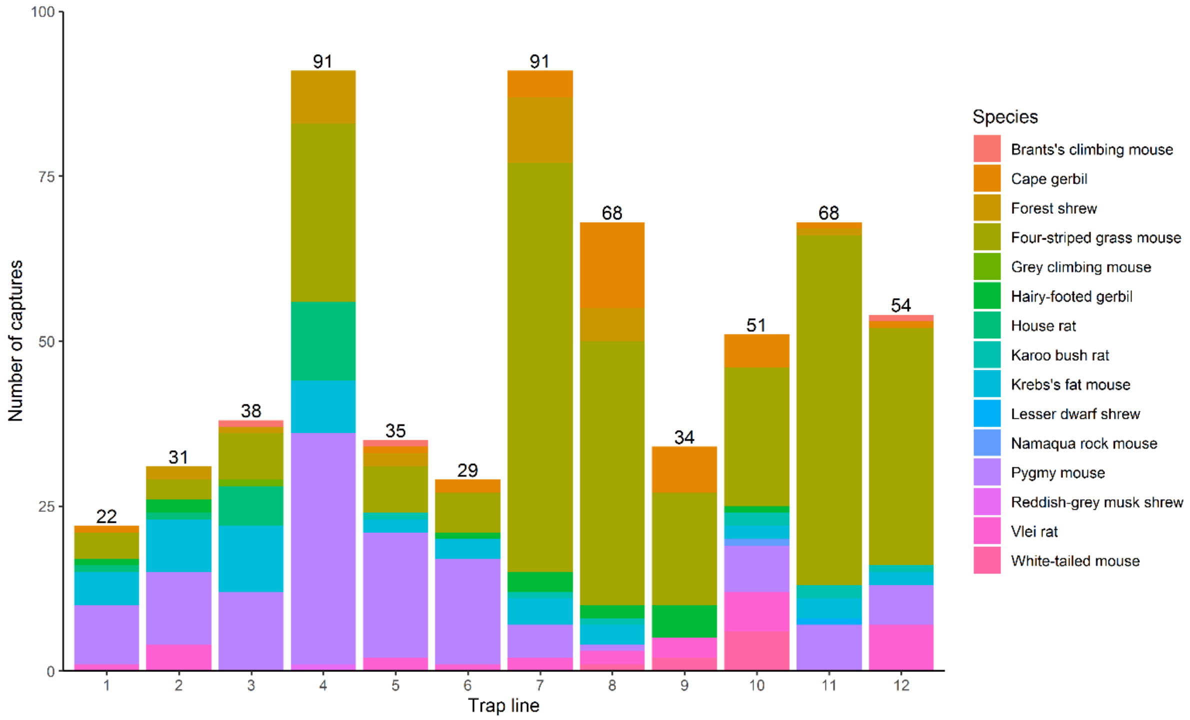


Figure 3.5: The total number of unique captures of 15 species on six trap lines in Atlantic Beach Estate and six in Blaauwberg Nature Reserve, each of which was open for six nights. Trap lines numbered 1 to 6 were on the estate and numbers 7 to 12 were on the reserve.

Some species were found at only one site, or at only one trap line within a site (Figure 3.6). Grey climbing mice, house rat and reddish-grey musk shrew were found only on the estate. The grey climbing mouse was found only at trap line 3, the reddish-grey musk shrew only on trap line 4, while house rats were found only on trap lines 1-4. Lesser dwarf shrew, Namaqua rock mouse and white-tailed rat were found only on the reserve. The lesser dwarf shrew was found only on trap line 11, the Namaqua rock mouse was found only on trap line 10, and the white-tailed rat was found only on trap lines 8-10.

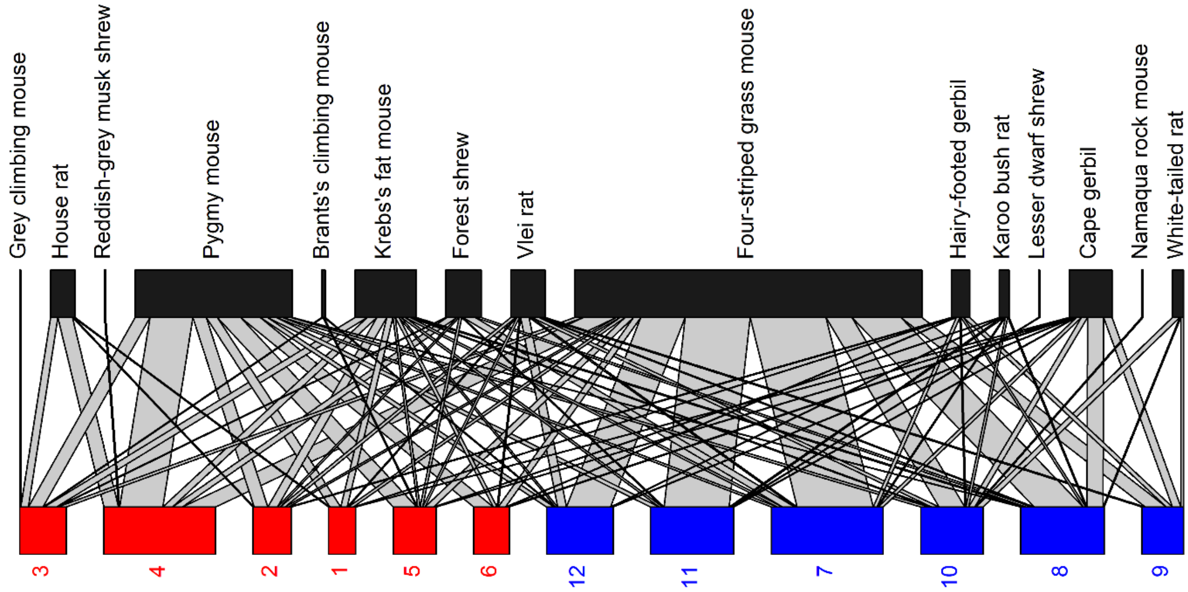


Figure 3.6: A bipartite interaction matrix showing how captured species are proportionally distributed across trap lines. Labels across the top of the plot are trapped species, while labels across the bottom are trap lines, with numbers 1 to 6 (shown in red) on Atlantic Beach Estate and numbers 7 to 12 (shown in blue) on Blaauwberg Nature Reserve. The width of the black box underneath each species shows the number of unique individuals of each species caught. The width of the red or blue box shows the number of unique individuals caught per trap line. The width of the webs joining species to trap lines is proportional and represents the number of individuals of a particular species caught on a particular trap line.

Recaptures

Species did not have an equal probability of recapture (Figure 3.7). Hairy-footed gerbil (*Gerbillurus paeba*) were the most likely to be recaptured, while house rats were the least likely. Some species were more likely to be recaptured on the estate, while others were more likely to be recaptured on the reserve (Figure 3.8).

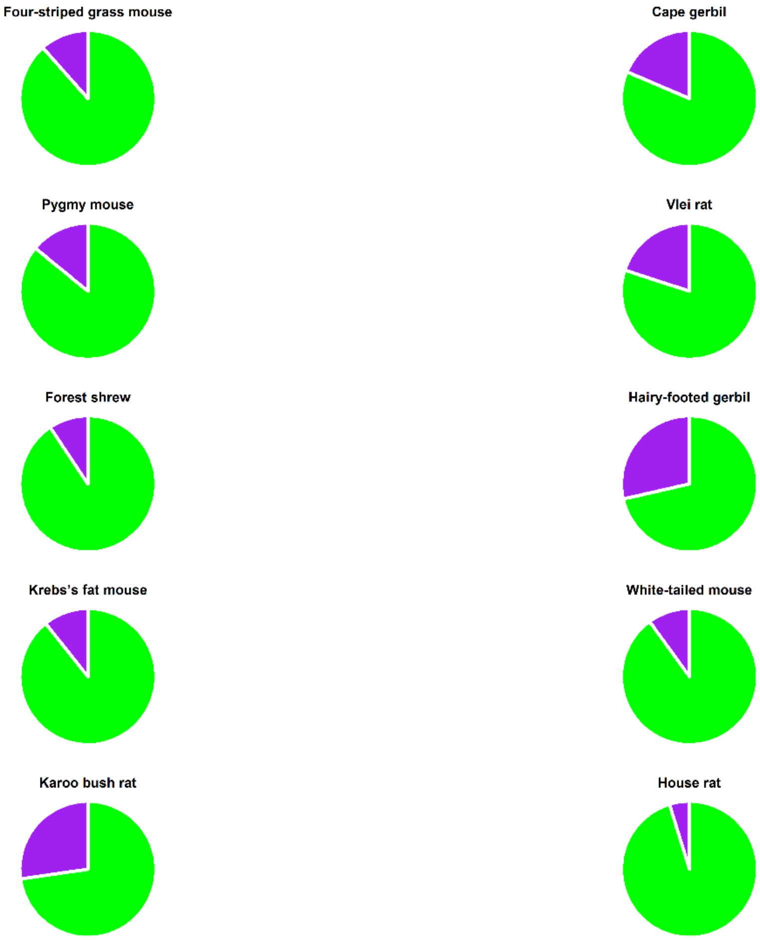


Figure 3.7: Proportion of independent captures (i.e., minimum number alive; green) and recaptures (purple) for the 10 species which had at least one recapture. Cumulatively the minimum number alive and the number of recaptures make the total number of captures.

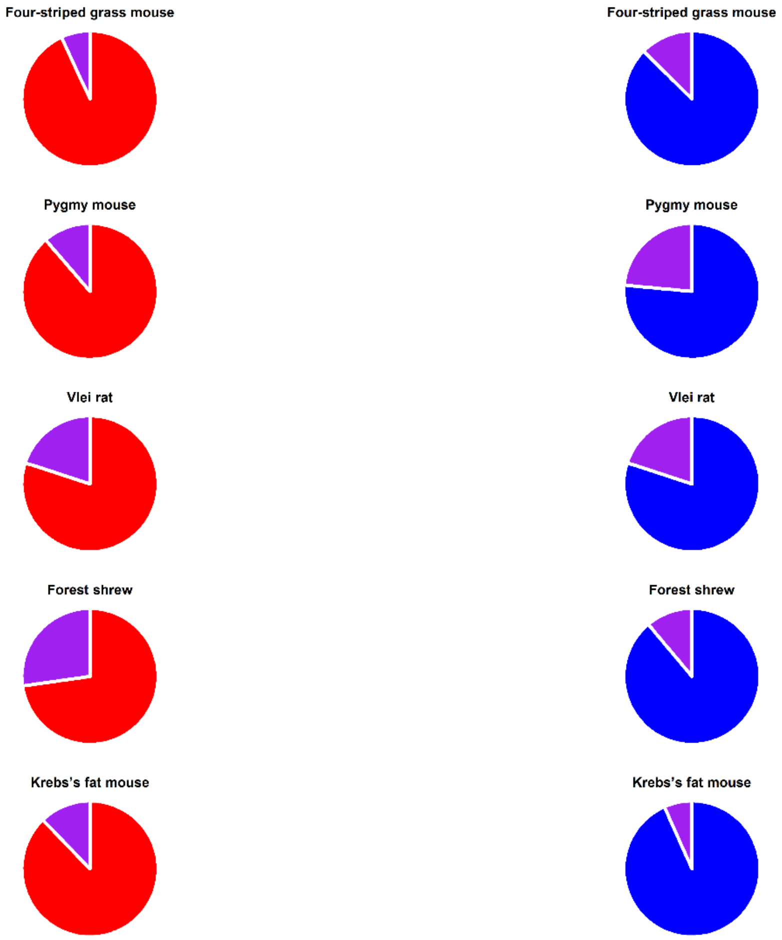


Figure 3.8: Proportion of independent captures (i.e., minimum number alive; red or blue) and recaptures (purple) for the five shared species with more than five captures and at least one recapture at both sites. Cumulatively the minimum number alive and the number of recaptures equal the total number of captures. Species caught in Atlantic Beach Estate are shown in red, while species caught in Blaauwberg Nature Reserve are shown in blue.

Body mass

There was no significant difference in body mass between any of the species I captured on at least five occasions at both sites (namely forest shrew, four-striped grass mouse, Krebs's fat mouse, pygmy mouse and vlei rat) (Figure 3.9, Appendix 3.1).

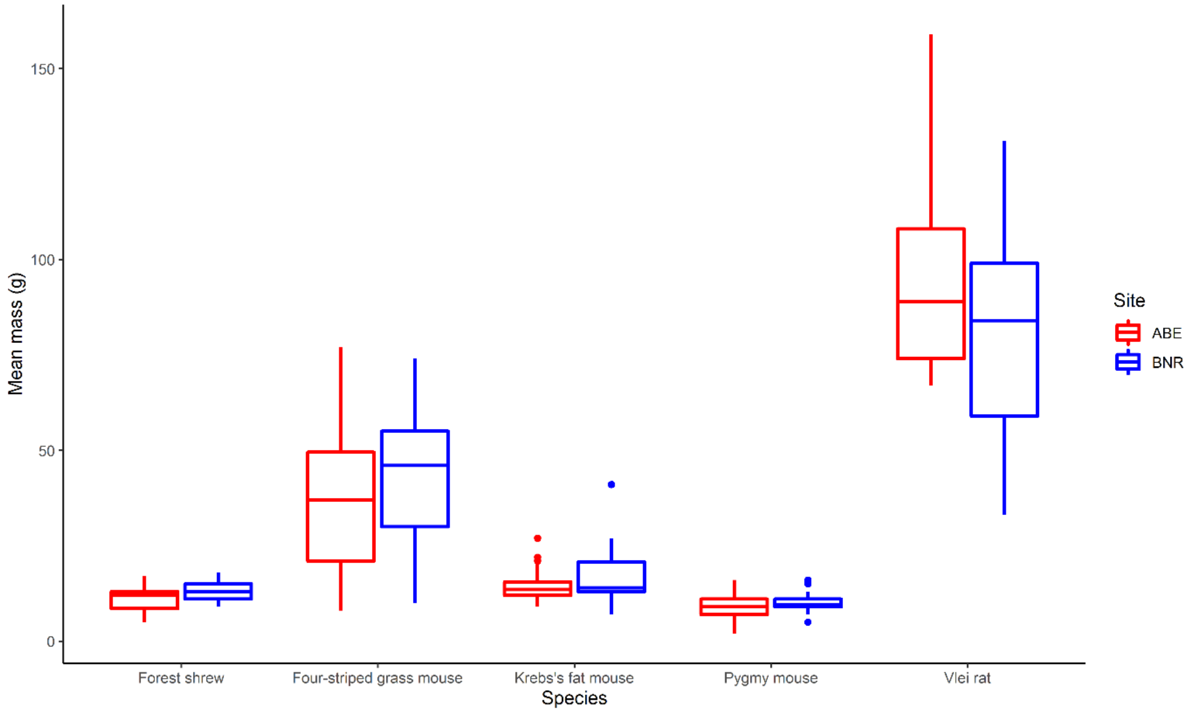


Figure 3.9: Mean mass (grams) of species with more than five captures at both Atlantic Beach Estate (ABE, red) and Blaauwberg Nature Reserve (BNR, blue).

Cumulatively, the small mammal biomass on the estate was lower than on the reserve (Table 3.5). This relationship held even when controlling for the different number of captures by calculating a "mean biomass", which effectively standardises the number of captures to allow for between site biomass comparisons. Mean biomass differed significantly between sites (W=17758, p-value<0.001), and was lower on the estate (27.32g), than the reserve (45.26g). In general, species which occurred at both sites had similar body masses (Table 3.5) with no clear trend for a given species between sites. Many species displayed large variation in mass, resulting in high standard deviations both within and between sites.

Table 3.5: Total and mean body mass (in grams + SD) of all species captured on Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR).

Species	**ABE**			**BNR**		
	Total	**Mean**	**SD**	**Total**	**Mean**	**SD**
Four-striped grass mouse (*R. pumilio*)	1794	38.17	17.62	8764	42.54	15.59
Cape gerbil (*T. afra*)	322	107.33	3.21	2196	95.47	21.23
Pygmy mouse (*M. minutoides*)	839	9.12	3.09	243	10.13	2.64
Vlei rat (*O. irroratus*)	679	97.00	33.86	1626	81.30	25.93
Forest shrew (*M. varius*)	134	11.17	4.02	173	13.31	2.84
Hairy-footed gerbil (*G. paeba*)	156	39.00	7.43	376	34.18	11.05
Krebs's fat mouse (*S. krebsii*)	467	14.59	3.86	243	17.36	8.94
White-tailed rat (*M. albicaudatus*)	-	-	-	616	68.44	32.29
Karoo bush rat (*O. unisulcatus*)	90	90.00	-	563	93.83	38.02
Brant's climbing mouse (*D. mesomelas*)	34	17.00	2.23	41[1]	41.00[1]	-
Lesser dwarf shrew (*S. varilla*)	-	-	-	4	4.00	-
Namaqua rock mouse (*M. namaquensis*)[2]	-	-	-	-	-	-
Grey climbing mouse (*D. melanotis*)	15	15.00	-	-	-	-
House rat (*R. rattus*)[3]	1333	102.54	61.70	-	-	-
Reddish-grey musk shrew (*C. cyanea*)	11	11.00	-	-	-	-
Total	5874			14845		
Mean		27.32			45.26	

[1] Assumed recording error.

[2] The Namaqua rock mouse escaped before being processed.

[3] Some house rats were too heavy for the scale (>200 g). All of these were given a mass = 200g.

Species richness, evenness and diversity

While the estate and the reserve had equivalent species richness, they differed in measures of species evenness and diversity (Table 3.6). The estate had higher evenness, Shannon-Wiener diversity and Brillouin index than the reserve, which had a higher Simpson's diversity.

Table 3.6: Species richness, evenness and diversity values for Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR). Pielou's evenness (J), Shannon-Wiener diversity index (H), Simpson diversity index (D) and the Brillouin index (Hb) are given.

	Species richness	**Pielou's evenness (J)**	**Shannon-Wiener diversity (H)**	**Simpson diversity (D)**	**Brillouin index (Hb)**
ABE	12	0.68	1.69	0.58	1.61
BNR	12	0.58	1.43	0.75	1.37

Trap lines had different numbers of species, with trap line 9 on the reserve having the lowest number of species (n=5), while trap line 10, also on the reserve, had the highest number (n=9) (Table 3.7). All trap lines on the estate had between 6 and 8 species (Table 3.7). Trap line 1 was predicted by iChao1 to have the highest number of species (n=12.72) while trap line 5 had the lowest predicted number of species (n=5).

Table 3.7: Observed species richness (Sobs), iChao1 estimate (including standard error (iChao1 (SE)), trap efficiency and effective number of species of trap lines on Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR).

Site	**Trap line**	**Sobs**	**iChao1**	**iChao1 (SE)**	**Trap efficiency**[1]	**Effective number of species**
ABE	1	7	12.72	6.77	0.55	-
ABE	2	7	7.24	0.71	0.97	-
ABE	3	7	9.92	4.33	0.71	-
ABE	4	6	6	0.48	1	-
ABE	5	8	9.46	2.24	0.85	-
ABE	6	6	8.31	3.62	0.72	-
ABE	All ABE trap lines	12	16.48	7.17	0.73	5.42
BNR	7	8	8.59	0.87	0.93	-
BNR	8	9	11.72	3.35	0.77	-
BNR	9	5	5	0.41	1	-
BNR	10	9	9.98	1.84	0.90	-
BNR	11	7	12.06	7.09	0.58	-
BNR	12	7	11.42	7.07	0.61	-
BNR	All BNR trap lines	12	14.99	4.5	0.8	4.18

[1] Trap efficiency is calculated as: Sobs/iChao1.

The estate and the reserve had the same gamma diversity (Table 3.8). However, at each trap line within the two sites, there was more variation in alpha and beta diversity. In addition, the proportional species turnover varied because of different alpha diversities on the different trap lines.

Table 3.8: Alpha, beta and gamma diversity as well as proportional species turnover for trap lines on Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR).

Site	Trap line	Alpha	Beta[1]	Gamma	Proportional species turnover[2]
ABE	1	7	1.71	-	0.42
ABE	2	7	1.71	-	0.42
ABE	3	7	1.71	-	0.42
ABE	4	6	2	-	0.5
ABE	5	8	1.5	-	0.33
ABE	6	6	2	-	0.5
ABE	All ABE trap lines	12	1	12	0
BNR	7	8	1.5	-	0.33
BNR	8	9	1.33	-	0.25
BNR	9	5	2.4	-	0.58
BNR	10	9	1.33	-	0.25
BNR	11	7	1.71	-	0.42
BNR	12	7	1.71	-	0.42
BNR	All BNR trap lines	12	1	12	0

[1] Beta diversity is calculated as gamma/alpha.

[2] Proportional species turnover is calculated as 1-alpha/gamma.

Differences between trap lines

In general, trap lines within sites were more similar than trap lines between sites. Within the estate comparisons varied between a minimum similarity of 34 % and a maximum similarity of 95 %, with an average of 60 % (Table 3.9). Comparisons between the estate and the reserve varied from a minimum similarity of 13% and a maximum similarity of 100 % between trap lines 5 and 12, and an average of 56 % (Table 3.9). Within reserve comparisons varied between a minimum similarity of 24 % and a maximum similarity of 99 %, with an average of 63 %. The overall average similarity percentage was 58 %.

Table 3.9: Sorensen pairwise similarity matrix for Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR). Trap lines which are similar in terms of species composition have similarity scores near 1, while trap lines which are different are close to 0. The average pairwise similarity was 0.58.

		ABE						**BNR**					
		1	2	3	4	5	6	7	8	9	10	11	12
ABE	1	1.00	0.89	0.35	0.43	0.54	0.95	0.84	0.74	0.77	0.78	0.33	0.49
	2		1.00	0.58	0.76	0.6	0.79	0.76	0.68	0.49	0.58	0.43	0.43
	3			1.00	0.63	0.62	0.34	0.43	0.38	0.13	0.3	0.38	0.38
	4				1.00	0.52	0.43	0.55	0.47	0.18	0.38	0.46	0.34
	5					1.00	0.58	0.93	0.95	0.42	0.72	0.65	1.00
	6						1.00	0.79	0.68	0.69	0.72	0.41	0.52
BNR	7							1.00	0.99	0.59	0.76	0.65	0.65
	8								1.00	0.62	0.85	0.66	0.62
	9									1.00	0.67	0.24	0.37
	10										1.00	0.51	0.74
	11											1.00	0.48
	12												1.00

There was generally less within site dissimilarity than between site dissimilarity and thus trap lines clustered according to site. Hierarchical clustering derived from a Euclidean dissimilarity matrix showed a clear separation of trap lines by site except for trapline 12 from the nature reserve which was more similar to traplines on the estate (Figure 3.10).

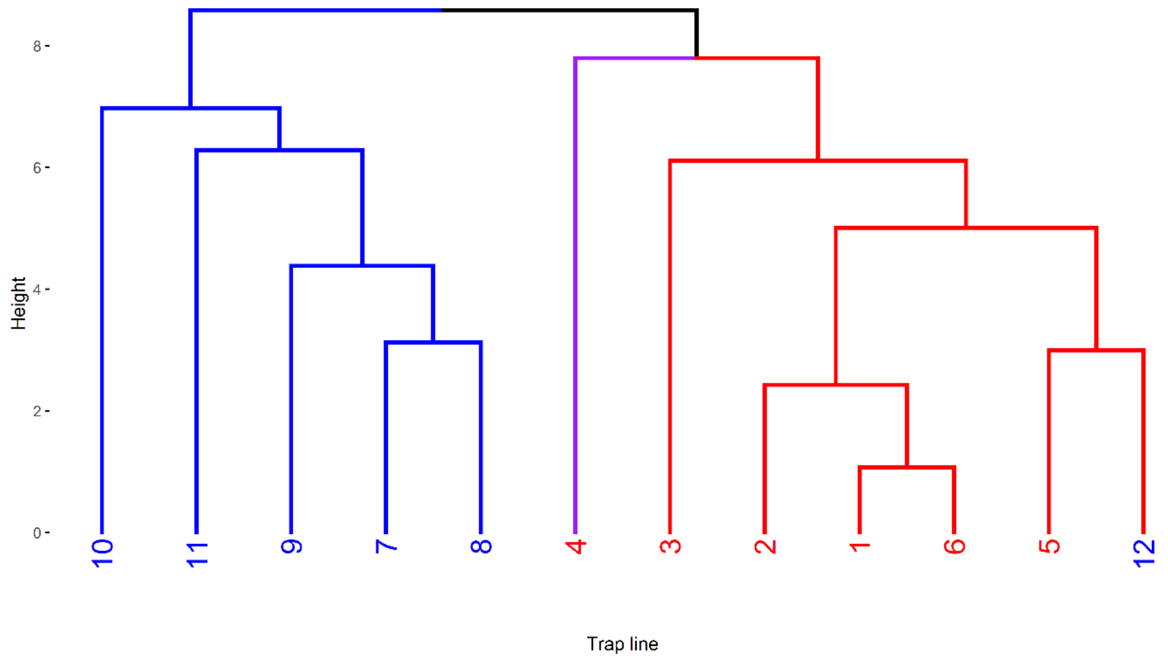


Figure 3.10: Cluster dendrogram for the 12 trap lines in Atlantic Beach Estate (numbers 1-6; in red) and Blaauwberg Nature Reserve (numbers 7-12; in blue).

Discussion

The mean trapping success of 21.5 % across both sites, is exceptionally high for Strandveld, where trapping success seldom exceeds 10 % (Steyn, 2013; G. Bronner, 2019, *pers. comm.*). Four-striped grass mice and Cape gerbil were the most abundant and second most abundant species in my trapping, both of which were recorded as the dominant species in a previous study with high abundance, sometimes to the detriment of other species (Rebelo *et al.*, 2019). While trapping success was much higher in the reserve the estate and the reserve nevertheless had the same number of species (n=12) and similar species composition, both results which were contrary to my predictions. Only one species on the estate was exotic (house rat), with the other two unique species the grey climbing mouse and the reddish-grey musk shrew, both being indigenous but known to persist in human modified landscapes (MacFayden and Relton, 2016; Taylor *et al.*, 2016a). The grey climbing mouse in particular is a habitat generalist and a pioneer species capable of persisting in both intact and degraded land (MacFayden and Relton, 2016). The low number of captures of this species may more be indicative of its semi-arboreal lifestyle and trap shyness as opposed to low abundance (Jooste and Palmer, 1982; MacFayden and Relton, 2016).

Another unexpected result was that the small mammal community on the estate was more even and more diverse across a range of metrics, including Pielou's evenness, Shannon-Wiener diversity and the Brillouin index. This suggests that while urban exploiting species may be present on the estate, they are not out-competing Strandveld specialists which have persisted despite the anthropogenic impacts.

As predicted, two generalist, pioneer species, the pygmy mouse and four-striped grass mouse, were the most abundant and second most abundant species on the estate respectively, cumulatively accounting for 63.4 % of the total number of independent captures on the estate. These two species were also abundant on the reserve, representing almost 70 % of the total number of independent captures with most captures (60 %) attributed to four-striped grass mice. Both species are generalist, pioneer species which dominate in disturbed habitats (Avenant, 2011; Rebelo *et al.*, 2019) and landscapes with high ground cover (Shanker, 2001) such as that in the reserve.

Unique species in the reserve included the white-tailed rat which is classified as "vulnerable" on the IUCN red list of threatened species (Avenant *et al.*, 2016). They are found primarily in the South African Highveld being grassland specialists, though a smaller, potentially relict population persists in the Western Cape (Dean, 1978) where they have a highly localized and patchy distribution (Avenant *et al.*, 2016). White-tailed mice have two distribution records from the Western Cape: in BNR, and in the far east of the province, alongside the border with the Eastern Cape (Avenant *et al.*, 2016). Of the records from BNR all of them occurred on Blaauwberg Hill, in the hill sector of the reserve. Hence these records represent a new capture location and the first captures in the last 13 years.

The two other species found only in the reserve, the lesser dwarf shrew and the Namaqua rock mouse have wide distributions across southern Africa (Russo *et al.*, 2016; Taylor *et al.,* 2016c). The lesser dwarf shrew is routinely found in gardens, so one would expect it to persist on the estate (Taylor *et al.,* 2016c). The Namaqua rock mouse is somewhat of an anomaly considering its preference for rocky habitats, and the lack of such habitats in the coastal sector of the reserve (Russo *et al.*, 2016).

Small mammal community composition is driven primarily by bottom-up ecological forces (Kerley, 1992; Meserve, Milstead and Gutiérrez, 2001) and thus differences in species composition between sites in the same area are likely to be driven by differences in vegetation and landscape characteristics between the two sites. The estate has retained patches of Strandveld but most of the land has been transformed for roads, the golf course and residential properties with the result that patches are largely isolated with limited movement between them recorded during the survey. In addition to habitat changes, ecological processes have also been altered with management on the estate practicing active fire suppression (Ecosense, 2012), while vegetation within the reserve is periodically subject to controlled burning (Küyler, 2011). Fire is critically important within the fynbos biome with many plant species requiring fire to complete their life cycles (Kruger and Bigalke, 1984). The lack of fire within the estate, and subsequent senescence of the natural vegetation may reduce the suitability of the remaining natural habitat to specialist species.

While not considered to be as important in regulating numbers, top-down regulation nevertheless does impact small mammal populations. In Chapter 4 I show that potential predators of small mammals are more abundant on the estate than in the reserve and includes novel exotics such as domestic dogs (*Canis lupus familiaris*) and cats. The latter in particular has been shown to pose a significant threat to biodiversity adjacent to and within residential areas of Cape Town (Seymour *et al.*, 2020) and elsewhere (Doherty *et al.*, 2016; Loss and Marra, 2017). Despite estate rules clearly stating that all pets must be restricted to residents properties unless they are under the control of their owners (Atlantic Beach Homeowners Association, 2013), domestic cats were the most active free ranging mammal on public open spaces within the estate (van Wyk, 2017; Chapter 4). Stricter enforcement of rules regarding domestic cats on the estate may allow small mammal numbers on the estate to increase to levels more similar to those in the reserve.

In general trap lines within sites were more similar to one another than between sites. The only exception to this was trap line 5 on the estate which was more similar to trap line 12 on the reserve than to the other trap lines on the estate. This trap line was along the perimeter of the estate bordering the nature reserve and because the fence does not represent a barrier for small mammals it is likely that there is movement between the reserve and this patch of natural vegetation in the estate. All other trap lines in the estate were located further from the estate boundary and this relative isolation from the reserve is reflected in a divergent small community (Baker *et al.*, 2003). Improved connectivity between patches within the estate and with the reserve may ensure greater movement between the reserve and the estate (Bennett, 1990; Beier and Noss, 1998) and thus buffer both communities from future stochastic events that may deplete genetic variation or cause local extinctions (e.g., excessive predation).

The most distinct trap line across both sites was trap line 4 which accounted for 55 % of the total unique captures of house rats, had the only capture of a reddish-grey musk shrew and had more than twice as many captures as any other trap line on the estate. Being at the centre of the estate and thus close to human habitation, this trap line was the most likely to have access to supplementary food resources including waste foods which may explain both the higher capture rate and the presence of commensal rats and shrews that favour protein rich food sources associated with human habitation (Taylor *et al.*, 2016b).

Rarefaction curves for both sites and increasing trap success in the reserve with calendar days both suggest that the methods for sampling small mammals in this study need to be adapted. Greater sampling effort is required at both sites and a longer period of habituation to traps and human activity is required in the reserve. Furthermore, despite opening traps within two hours of dusk and checking them in the four hours after dawn, my sampling was biased to nocturnal species with traps closed for much of the day to avoid trap mortalities associated with high daytime temperatures. Additionally, despite expected mole and molerat presence, we did not capture any individuals from these taxa. Sherman traps, although able to catch moles and molerats, do so infrequently, and more target specific traps would likely be more effective (G. Bronner, 2019, *pers. comm*.).

Despite extreme modification of much of the land on the estate and the introduction of new predators this site still supports most of the species (9/12) which occurred on the nature reserve, and two unique indigenous species viz., the grey climbing mouse and reddish-grey musk shrew. One vulnerable species, the white-tailed rat was absent from the estate and an exotic invasive species, the house rat had been introduced. Together these findings suggest that small mammals can persist within golfing eco-estates that include patches of indigenous vegetation with patches closest to intact natural areas having more similar species composition than those that are more isolated and surrounded by dense residential areas.

Appendix 3.1 Supplementary tables and figures

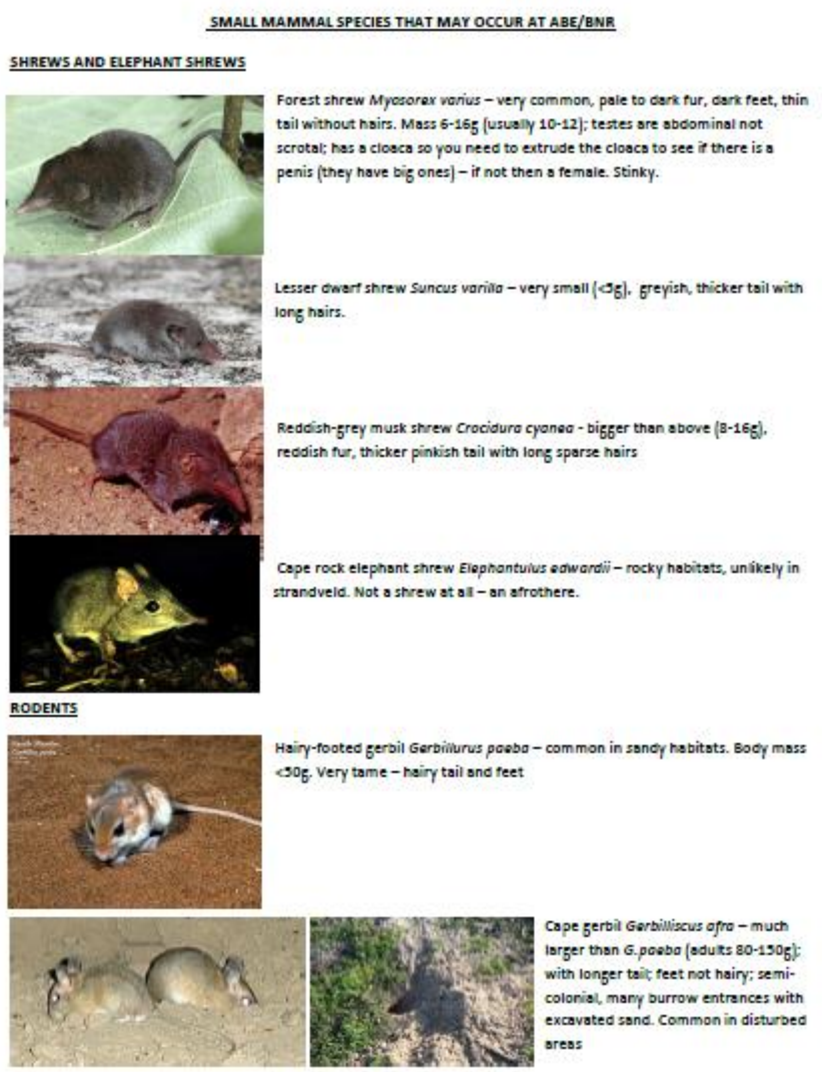
Table S3.1.1: GPS coordinates for the start and end of every trap line on Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR).

Site	**Trap line**	**Start trap line GPS**		**End trap line GPS**	
		X	**Y**	**X**	**Y**
ABE	1	18.444327	-33.739611	18.443828	-33.735507
ABE	2	18.444644	-33.739584	18.444544	-33.735247
ABE	3	18.448533	-33.741522	18.447992	-33.739217
ABE	4	18.446551	-33.745590	18.449652	-33.743964
ABE	5	18.450031	-33.749153	18.446467	-33.746885
ABE	6	18.450273	-33.750864	18.447282	-33.747971
BNR	7	18.449908	-33.767966	18.448734	-33.764760
BNR	8	18.451016	-33.768285	18.449992	-33.764708
BNR	9	18.455874	-33.769728	18.456056	-33.766235
BNR	10	18.453686	-33.772883	18.457489	-33.770705
BNR	11	18.458244	-33.777714	18.454505	-33.775737
BNR	12	18.458220	-33.776744	18.454285	-33.775213

Table S3.1.2: Statistical test for differences in mean biomass for species between sites (see Figure 3.9). Data were first screened for normality and tested accordingly. The appropriate test statistic and p-value are presented.

Species	**Test**	**Test statistic**	**p-value**
Forest shrew	Welch Two Sample t-test	t=-1.5269	0.1427
Four-striped grass mouse	Asymptotic Wilcoxon rank sum test	W=4045.5	0.07874
Krebs's fat mouse	Asymptotic Wilcoxon rank sum test	W=199	0.5554
Pygmy mouse	Asymptotic Wilcoxon rank sum test	W=887	0.1354
Vlei rat	Welch Two Sample t-test	t=1.1174	0.2941

Appendix 3.2 Identification guide



SMALL MAMMAL SPECIES THAT MAY OCCUR AT ABE/BNR

SHREWS AND ELEPHANT SHREWS

Forest shrew *Myosorex varius* – very common, pale to dark fur, dark feet, thin tail without hairs. Mass 6-16g (usually 10-12); testes are abdominal not scrotal; has a cloaca so you need to extrude the cloaca to see if there is a penis (they have big ones) – if not then a female. Stinky.

Lesser dwarf shrew *Suncus varilla* – very small (<5g), greyish, thicker tail with long hairs.

Reddish-grey musk shrew *Crocidura cyanea* - bigger than above (8-16g), reddish fur, thicker pinkish tail with long sparse hairs

Cape rock elephant shrew *Elephantulus edwardii* – rocky habitats, unlikely in strandveld. Not a shrew at all – an afrothere.

RODENTS

Hairy-footed gerbil *Gerbillurus paeba* – common in sandy habitats. Body mass <50g. Very tame – hairy tail and feet

Cape gerbil *Gerbilliscus afra* – much larger than *G.paeba* (adults 80-150g); with longer tail; feet not hairy; semi-colonial, many burrow entrances with excavated sand. Common in disturbed areas

Pygmy mouse *Mus minutoides* – all habitats (<10g vs. >12g in *S. krebsii*). Paler than Fat mouse, chestnut-brown above and whitish below.

Fat mouse *Steatomys krebsii* – sandy habitats (>12g), thicker tail and paler colour than *M.minutoides*. Trap-shy

Striped mouse *Rhabdomys pumilio* – all habitats

Vlei rat *Otomys irroratus* – more mesic habitats but also far from water. Note large ears and eyes, short tail. Darker colour than *O. unisulcatus*, does not make stick nests. But both spp. very trap-shy.

Karoo bush rat *Otomys unisulcatus* – paler than vlei rat. Makes stick nests in bushes. Count how many you see on your traplines!

Grey Climbing mouse *Dendromys melanotis* – differs from *D. mesomelas* which has chestnut colour. Both spp. are trap-shy and usually found in bushes rather than on the ground.

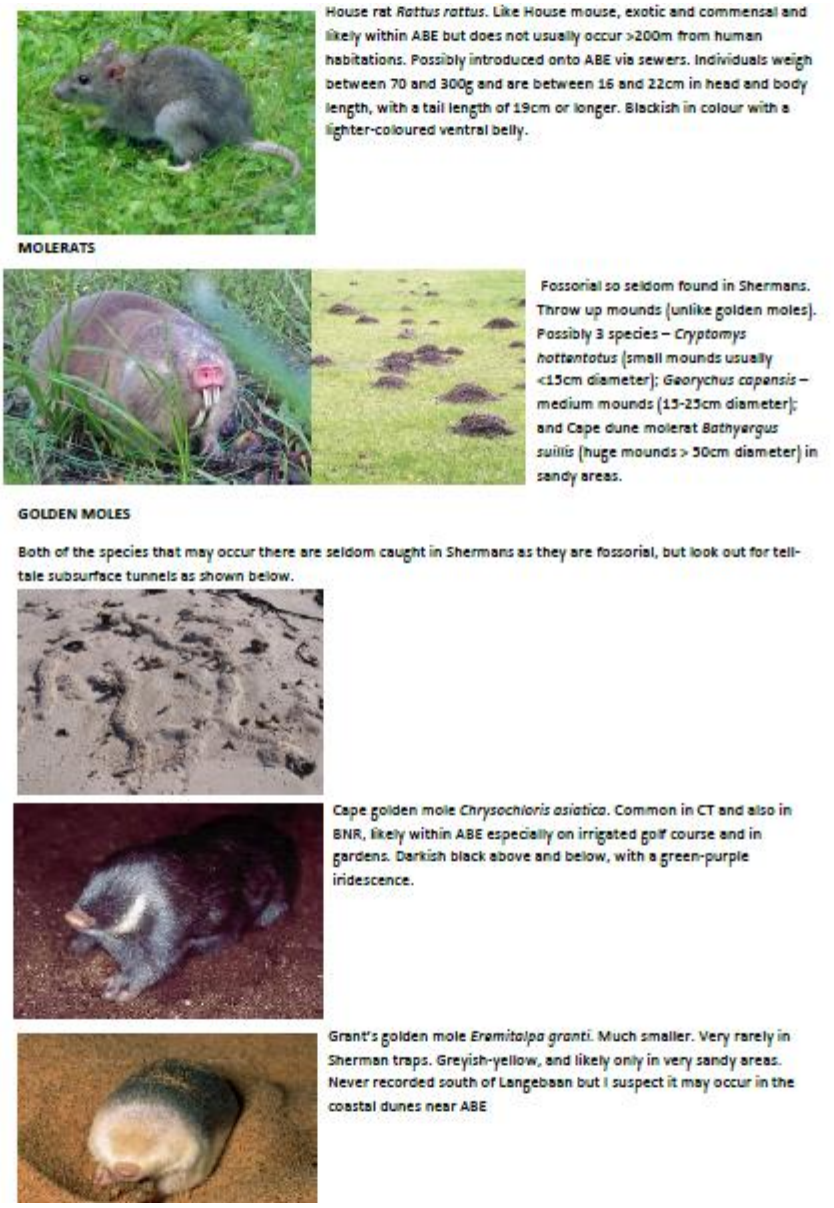
Brandt's climbing mouse *Dendeomus mesomelas* – note chestnet colour.

Large-eared mouse *Malacothrix typica* – rare in traps, greyish with black back stripe and large ears. Actually very common in strandveld but seldom enters traps so numbers underestimated.

Namaqua rock rat *Micaelamys namaquensis* – rocky habitats (long tail). Unlikely in strandveld habitats.

White-tailed mouse *Mystromys albicaudatus*. Dorsally buffy-grey with speckles of black. Both the tail and the underside are white. Head and body is 14 - 18 cm, tail 5-8 cm. Body mass 78-96 g. Reported to occur at BNR but not confirmed and I doubt it as it is a montane species in WC.

House mouse *Mus musculus*. Exotic and human commensal, likely on ABE but not BNR as they seldom occur>200m from houses. 65-95 mm long plus tail 60-105 mm. Fur ranges from light brown to black with white or buffy bellies. 12 to 30 g.



House rat *Rattus rattus*. Like House mouse, exotic and commensal and likely within ABE but does not usually occur >200m from human habitations. Possibly introduced onto ABE via sewers. Individuals weigh between 70 and 300g and are between 16 and 22cm in head and body length, with a tail length of 19cm or longer. Blackish in colour with a lighter-coloured ventral belly.

MOLERATS

Fossorial so seldom found in Shermans. Throw up mounds (unlike golden moles). Possibly 3 species – *Cryptomys hottentotus* (small mounds usually <15cm diameter); *Georychus capensis* – medium mounds (15-25cm diameter); and Cape dune molerat *Bathyergus suillis* (huge mounds > 50cm diameter) in sandy areas.

GOLDEN MOLES

Both of the species that may occur there are seldom caught in Shermans as they are fossorial, but look out for tell-tale subsurface tunnels as shown below.

Cape golden mole *Chrysochloris asiatica*. Common in CT and also in BNR, likely within ABE especially on irrigated golf course and in gardens. Darkish black above and below, with a green-purple iridescence.

Grant's golden mole *Eremitalpa granti*. Much smaller. Very rarely in Sherman traps. Greyish-yellow, and likely only in very sandy areas. Never recorded south of Langebaan but I suspect it may occur in the coastal dunes near ABE

Figure S3.2.1: Identification guide used in addition to the field guide.

CHAPTER 4: Mammals

Abstract

Urbanisation typically has a negative impact on the diversity and abundance of mammals but select species may benefit through access to anthropogenic resources and the elimination of predators and competitors. In this chapter I explored how land use influences mammals by comparing the diversity, abundance and occupancy of mammals in a fenced golfing eco-estate (Atlantic Beach Estate) with a neighbouring small open nature reserve (Blaauwberg Nature Reserve) on the edge of the City of Cape Town. I deployed 25 camera traps in patches of natural habitat and green open spaces within the estate and mirrored this configuration in the reserve. Camera traps were active for 1555 trap nights between the two sites (n=776 on the estate and n=779 on the reserve) in September and October 2019. The estate and the reserve had a similar number of mammal species (n=8 and n=9), though half the species on the estate were either domestic animals, or introduced species, none of which were found in the reserve. Domestic cats (*Felis catus*), which are prolific predators, were found ubiquitously across the estate. Humans were the most frequently photographed mammal on the estate (Relative abundance index (RAI)=135.44), followed by Cape grysbok (*Raphicerus melanotis*) (RAI=65.21) and springbok (*Antidorcas marsupialis*) (RAI=50.39). Common duiker (*Sylvicapra grimmia*) was the most frequently photographed mammal on the reserve (RAI=30.55), followed by both Cape grey mongoose (*Herpestes pulverulentus*) and steenbok (*Raphicerus campestris*) (RAI=6.93). Probability of use on the estate was best explained by human RAI while Normalized Difference Vegetation Index (NDVI) was the best predictor of probability of use within the reserve. Cape grysbok on the estate displayed a noticeable shift toward nocturnality presumably to avoid the diurnal peak in human activity. While eco-estates estates can clearly sustain a subset of native and non-native mammal populations the limited connectivity with other populations, imposed by the estate boundary fence reduces their conservation value. Importantly no domestic animals were recorded in the reserve suggesting that the fence reduces their impact on fauna in the neighbouring reserve.

Introduction

The impacts of urbanization are varied and depend primarily upon the characteristics of the urban habitat and of the species in question (McKinney, 2002, 2006, 2008). In general, as the proportion of natural land decreases and consequently human modified land increases, mammal species richness decreases (McKinney, 2006). Specialist species are usually replaced by generalist species, which often include exotic species that may competitively exclude native species, if they are capable of benefitting from transformed habitats and the novel food and shelter urban areas provide (McKinney, 2002). However, this may be somewhat offset by the retention of important patches of naturally occurring vegetation, and connectivity between patches (Beninde, Veith and Hochkirch, 2015; Downs *et al.*, 2021). There are three main responses displayed by individual species to urban areas: urban exploiters thrive, urban tolerators persist and urban avoiders escape (Blair, 1996; McKinney, 2002). Overall, species which are habitat specialists are more likely to be extirpated, while generalists are more likely to thrive (Ramesh, Kalle and Downs, 2016; Ehlers Smith *et al.*, 2020). Furthermore, some species may be located only within patches of natural vegetation, while other species may be found throughout the urban matrix (Alexander *et al.*, 2019a, 2019c; Zungu *et al.*, 2020).

There is increasing awareness about the ability of urban areas to conserve biological diversity, including medium-large mammalian species, in the urban mosaic and also the necessity of conservation efforts within these spaces to ensure this happens (Soanes and Lentini, 2019). Nowhere is this more prevalent than on eco-estates, which seek to provide both space for human settlement, but also suitable habitat for wildlife (Grey-Ross, Downs and Kirkman, 2009; Sherriff-Shüping, 2015). Eco-estates typically contain less dense settlements and increased habitat for wildlife and as a result have the potential to harbor meaningful mammal populations, if they successfully maintain habitat connectivity through corridors, and large natural patches (Beninde, Veith and Hochkirch, 2015; Mistry and Spocter, 2020; Downs *et al.*, 2021). Research on mammal persistence on eco-estates in South Africa has occurred primarily in Kwa-Zulu Natal (KZN), and has focused on the space use (e.g., Patterson, Kalle, & Downs, (2019)) or functional diversity (e.g., Alexander, Ehlers Smith, Ehlers Smith, & Downs (2019)) of individual species or communities within eco-estates. When mammal communities on eco-estate have been compared to surrounding land, it has generally been to agricultural land or urban areas, and hence may not be an accurate reflection of how well mammal species could persist in a relatively undisturbed site (Alexander *et al.*, 2019a, 2019c).

While the extirpation from an area or reduced prevalence of a species across a landscape is indicative of important differences between communities, there are other important metrics of population status. Disturbance in a landscape often results in changes to animal activity patterns (Ogutu *et al.*, 2014; Palacín *et al.*, 2017). These changes have predominantly been quantified spatially, with animals relocating into or out of areas which have been disturbed by humans (Frid and Dill, 2002; Tucker *et al.*, 2018). However, humans can also cause changes in the temporal activity of animals in places where animals cannot spatially escape humans (Ramesh and Downs, 2013; Gaynor *et al.*, 2018; Searle *et al.*, 2021). In many mammal species, high human disturbance promotes increased nocturnality as animals attempt to temporally avoid humans (Gaynor *et al.*, 2018; Johann *et al.*, 2020). This shift to nocturnality can have numerous costs including altered species interactions, decreasing foraging efficiency, diminished antipredator strategies and increased metabolic energy expenditure, all of which can carry a survival and fitness cost (Werner and Peacor, 2003; Gaynor *et al.*, 2018). Shifting towards a more nocturnal activity pattern may be indicative of additional stressors being placed on animals by sustained human presence. While the monitoring of mammals on eco-estates is increasing, studies have focused on space use or functional diversity and hence may have overlooked potential signs of stress in mammals residing on eco-estates.

Monitoring mammals on the estate and the reserve

In 2017 the ABE Homeowners Association, in conjunction with the City of Cape Town and the Cape Town Environmental Education Trust, commissioned a camera trap survey of the estate and the neighbouring reserve. The survey was initiated in response to increased domestic cat (*Felis catus*) predation on the estate by caracal, though the study also aimed to compare the activity of fauna on the estate with that of the reserve and to provide data on species presence for comparisons with other City of Cape Town reserves (van Wyk, 2017).

Rationale, aims and predictions

Eco-estates are likely to become increasingly prevalent, with mounting pressure from developers to build on previously undeveloped sites. Some these sites may include ecologically sensitive land and the hope is that eco-estates will provide a refuge for wildlife in a peri-urban setting. It is therefore important to quantify the impacts of such developments on biological diversity and medium-large mammals in particular. The aim of this chapter is to quantify differences in medium-large mammal communities between the Atlantic Beach Estate and the neighbouring Blaauwberg Nature Reserve. Medium-large mammals generally persist better in larger, contiguous, natural habitats with less human disturbance than smaller, fragmented habitats frequented by people, pets and vehicles (Diamond, 1975; Brooks *et al.*, 2002; Thornton, Branch and Sunquist, 2011). As such, I predict a higher species richness of native species and increased probability of use on the reserve as opposed to the estate. Additionally, I expect that species on the estate will show an observable shift towards nocturnality in the presence of high human activity during the daytime.

Methods

Camera traps

Through recent technological advances, camera traps have become firmly established tools for gathering data on the presence, distribution and habitat use of mammals (Meek and Fleming, 2014). Camera traps are advantageous in that they provide both spatial and temporal information, are less invasive than most other methods, are less costly and time consuming and they can be deployed with only minimal training (Cutler and Swann, 1999). Camera traps are also useful for monitoring the status of wildlife species because they collect information at the scale of populations rather than individuals. In addition, utilising camera traps allows for 24-hour, year round monitoring of species (Cutler and Swann, 1999), which is particularly useful for nocturnal species, species with clear seasonal differences in presence and those with a fear of humans or that are especially rare and hence may be missed with shorter duration surveys (Meek and Fleming, 2014; Wearn and Glover-Kapfer, 2017). Camera trapping also has lower between observer error, provided the camera traps are deployed systematically (Meek and Fleming, 2014). Despite these advantages camera traps are nevertheless considered to be "imperfect observers" (Lyra-Jorge *et al.*, 2008) and may fail to record an animal for various reasons, including failing to trigger a camera because of animal size or movement characteristics (Caravaggi *et al.*, 2017) or avoiding the camera's detection zone (Burton *et al.*, 2015). Cameras may also be stolen, dislodged by other wildlife and fail in weather extremes.

Camera trap survey design

I did not consider all the land within the estate to be suitable for camera trapping. Residential properties, buildings, roads and other estate facilities (such as tennis courts and golf fairways and greens) cannot sustain mammal populations in this context or are unsuitable for camera trap placement, and hence these areas were excluded from the survey area. The small size of residential gardens, which often contained domestic animals, and because the estate functions as a larger communal "garden" meant gardens were excluded from camera placement, though I recognize that they can harbour significant biodiversity in other contexts (Van Helden, Close and Steven, 2020). Camera traps were thus only placed in the remnant patches of natural habitat and the edge of the golf course (within 5 m; henceforth termed "buffer zone"). I allocated camera traps within estate habitats (namely remnant Strandveld and buffer zone) based on the relative proportion of each land cover type. Natural areas cumulatively cover 493 075 m^2, while buffer zones cover 69 207 m^2 resulting in 22 camera traps placed in Strandveld patches and three in the buffer zone. Camera stations were a minimum of 200 m apart. I used the same number of camera traps within the reserve (n=25) to standardise for effort and mirrored the configuration in the estate within the reserve (Figure 4.1).

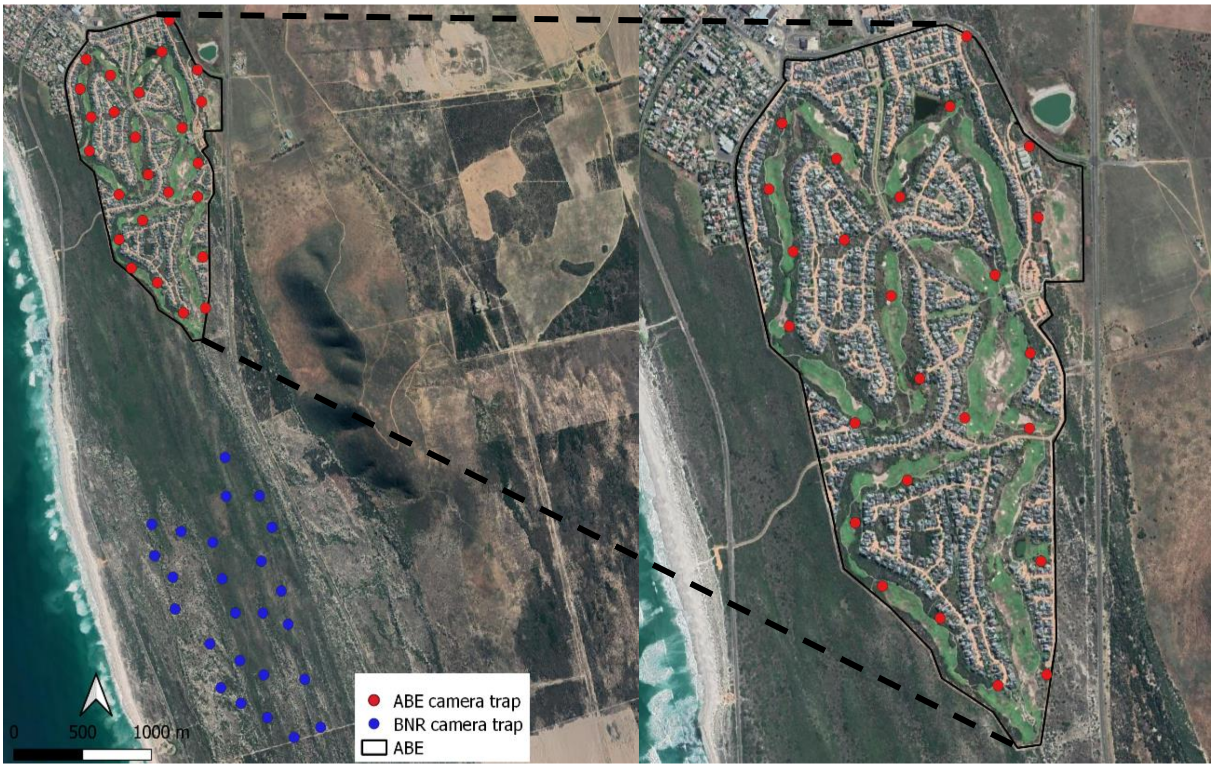


Figure 4.1: Camera trap stations on Atlantic Beach Estate (ABE, top cluster of points) and Blaauwberg Nature Reserve (BNR, lower cluster of points; mirror of top cluster) with the insert showing a magnified view of the ABE camera stations.

Fine scale camera trap placement significantly impacts capture probabilities and completeness of species inventories (Colyn, Radloff and O'Riain, 2018). I thus attempted to optimise photographic captures of animals by placing cameras along game trails with a good field of view, ideally with evidence of spoor or scat, but always within 20 m of the mapped global positioning system coordinate.

I deployed a single infrared flash equipped Bushnell Trophy Cam HD camera trap (Bushnell Corporation, Overland Park, Kansas) at each station. This allowed the capture of photographs both during the day and at night with minimal disturbance of animals and of residents (Rovero *et al.*, 2013; Henrich *et al.*, 2020). I attached camera traps to metal stakes planted in the ground, or to suitable natural structures (e.g., trees). I placed cameras approximately 30 cm off the ground to maximize captures of small to medium sized mammals (Kelly, 2008). By placing cameras in areas which were naturally more open, I minimized the amount of vegetation that had to be cleared, while simultaneously reducing false positive images linked to moving vegetation (Swann *et al.*, 2004).

My camera trap survey was conducted over a 42-day period (from the 10th of September to the 20th of October 2019; Table 4.1). All cameras were active for a continuous period of 30 days (11 September to 11 October) to prevent violating the assumption of population closure (O'Connell, Nichols and Karanth, 2011). I checked all camera traps approximately halfway through the survey and replaced non-functioning cameras and batteries that were low on charge. I switched out SD cards in cases where the camera had recorded more than 1000 photographs, and changed the batteries on a single camera, which had no bars of battery remaining, but was still operational.

Table 4.1: Camera trap survey details for stations on Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR).

Site	No. of stations	Start date	End date	No. of trap nights
ABE	25	10 September 2019	11 October 2019	776
BNR	25	11 September 2019	20 October 2019[1]	779

[1] BNR cameras were taken down over multiple days. 24/25 cameras were down by the 15th of October 2019.

Table 4.2: Key camera trap settings applied to all cameras.

Parameter	Setting
Resolution[1]	8/12/16 megapixels
Interval	30 seconds
Sensor level	Auto
NV shutter	Medium

[1] Image resolution was dependent on which camera trap model I used. In all cases I used the highest available resolution on a camera.

Data analyses

I systematically deleted blank images triggered by vegetation movement, before importing the images into CameraBase (version 1.7 (Tobler, 2013)). I considered individuals of a species to be "independent" if captures at a station occurred more than 30 minutes apart (O'Brien, Kinnaird and Wibisono, 2003). Once an individual or group from a certain species had been recorded at a station, I regarded any further image(s) of that species at that station as a "duplicate" if it was within 30-minutes of the previous image. In cases where individuals from a species are individually recognizable (e.g., humans or domestic cats), multiple individuals could be recorded within a 30-minute time frame, provided they were different individuals. When encountering group living animals, I estimated group size based on all the available pictures of that particular group. Group size may therefore be higher than the number of individuals captured in any one image.

To assess whether I had adequately sampled my two sites, I performed site-based rarefaction analyses using the *vegan* package (Oksanen *et al.*, 2019). I calculated the relative abundance index (RAI) for all terrestrial mammals at each site. Species RAI is the total number of independent captures of a particular species divided by the total number of trap nights for a particular site (ABE or BNR) and standardized by effort (multiplied by 100):

$$\frac{total\ number\ of\ independent\ captures}{site\ trap\ nights}\ x\ 100$$

Occupancy / Probability of use

Occupancy is defined as the “proportion of area, patches or sampling units that is occupied (i.e., species presence)” (MacKenzie *et al.*, 2006). Occupancy is considered a state variable, in that one can use occupancy to quantify a dynamic system at a fixed point in time (MacKenzie *et al.*, 2006). It would be easy to assume that occupancy (ψ) is merely the number of sites where the species is present (x) divided by the total number of sites (s):

$$\psi = \frac{x}{s}$$

This equation would yield the proportion of sites occupied by a species. However, this equation represents the occupancy of a species in an area under perfect detection (i.e., where all individuals in the sample area are detected with absolute certainty), known as the naïve occupancy. Occupancy models attempt to estimate occupancy (ψ) as a function of various covariates (e.g., environmental and habitat characteristics) under the assumption that species are imperfectly detected (because of site level environmental covariates and survey specific covariates), but that detectability can be estimated based on repeated site visits (MacKenzie *et al.*, 2002; Guillera-Arroita, 2017; Gould *et al.*, 2019).

Camera traps are ideally suited to collect data for use in occupancy modelling and have been frequently been used for this purpose when studying mammals in South Africa (Thorn *et al.*, 2009; Ramesh and Downs, 2015; Rich *et al.*, 2017; Colyn, Radloff and O’Riain, 2018; Drouilly, Clark and O’Riain, 2018; Rogan *et al.*, 2019; Schnetler, Radloff and O’Riain, 2020; Woodgate, Distiller and O’Riain, 2021). Camera traps encompass both components of an occupancy model: presence/absence data (which can later be modelled based on various covariates) and repeat visits, necessary to estimate detectability, as cameras are left in the field for many days, which can be split into appropriately sized sampling units.

Occupancy models have two basic assumptions: population closure (there are no changes in the population during the survey) and independence (between stations and across occasions) (Sollmann, 2018). Though occupancy models are robust to violation of these assumptions, in situations where these two assumptions are not met, estimates should be considered “probability of use” estimates as opposed to occupancy probability (MacKenzie and Royle, 2005; Kendall and White, 2009). Probability of use estimates are developed within the same framework as an occupancy model. Considering the small inter-trap distances in my camera trap array, I adopt probability of use estimates for each species, in this chapter.

Normalized Difference Vegetation Index (NDVI)

The influence of vegetation cover on species is inconsistent, with some species having a preference for areas of thick vegetation and high cover (e.g., Cape grysbok (Palmer *et al.*, 2016)), while others prefer more open habitats (e.g., steenbok (*Raphicerus campestris*) (Palmer, Birss and du Toit, 2016)). NDVI values have been found to increase with increasing plant cover (Martinuzzi *et al.*, 2008). NDVI can therefore be used as a proxy for vegetation cover and plant productivity and is calculated as:

$$\frac{NIR - red}{NIR + red}$$

where *NIR* is the near-infrared light, which plants largely absorb, and *red* light, which plants largely reflect, as measured by a satellite sensor (Pettorelli *et al.*, 2011). I used satellite imagery from the Sentinal 2 satellite at 10 m resolution taken during the camera trapping survey and later extracted through the *sen2r* package in R (Ranghetti and Busetto, 2020; Ranghetti *et al.*, 2020).

Distance to roads

Roads present direct and indirect dangers but they also serve as movement corridors and provide foraging opportunities on the edge for mammals (Spellerberg, 1998; Mann, O'Riain and Parker, 2015; Grilo *et al.*, 2020; Hill, De Vault and Belant, 2021). Major roads which have high traffic volumes and allow high speeds, such as those bordering my study site, have only detrimental effects on most mammal species (Grilo, Bissonette and Santos-Reis, 2008; Fahrig and Rytwinski, 2009; Collinson *et al.*, 2015; Hill, DeVault and Belant, 2019). Within the estate, the road network is denser than in the reserve, but the speed is limited to 20 km/h with dense vegetation next to the road. The risks of vehicle accidents for wildlife on the estate is lower than major roads, but still a distinct possibility. The coastal sector of reserve is bounded by two major roads which serve as the sector boundary. In essence, distance to roads reflects distance to edge of the reserve and hence susceptibility to edge effects, including increased levels of anthropogenic mortality (Woodroffe and Ginsberg, 1998; Massey, King and Foufopoulos, 2014; Hill, DeVault and Belant, 2019). I predicted a decrease in the probability of use by all species closer to roads because of the threat they pose. I scaled distance to roads for use in my probability of use models.

Human relative abundance index

Human activity can disrupt the behaviour of animals in a multitude of ways (Frid and Dill, 2002; Palacín *et al.*, 2017; Gaynor *et al.*, 2018). While some species can become habituated to or even attracted to humans who variously feed and provide shelter for a range of species in an urban context (Knight, 2009), most wild animals have an inherent fear of humans who fulfill the role of an apex predator in most systems (Frid and Dill, 2002; Smith *et al.*, 2017; Johann *et al.*, 2020). As a result, animals typically either spatially or temporally avoid humans (Frid and Dill, 2002; Gaynor *et al.*, 2018; Tucker *et al.*, 2018). By humans, I refer specifically to humans on foot, not human settlements. I predict an increase in activity of humans is likely to decrease the probability of use in all species. I calculated human RAI at each station as follows:

$$\frac{number\ of\ independent\ human\ captures\ at\ station}{station\ trap\ nights}\ x\ 100$$

I scaled human RAI values before incorporating them into my probability of use models.

Detection covariates (see Appendix 4.3 for values)

Camera

I used three different models of Bushnell camera traps, which were manufactured in 2012, 2016 and 2017 respectively. These models have different sensitivities and different fields of detection, which may impact upon detectability. I thus included camera model as a detection covariate.

NDVI

As previously discusses, NDVI is a proxy for vegetation cover and productivity. Areas with higher NDVI are likely to have more vegetation cover and hence reduced detection ability.

Probability of use models for frequently detected species

I fitted the single species, single season occupancy model of MacKenzie *et al.* (2002) in the *unmarked* package (Chandler *et al.*, 2020) for common duiker (*Sylvicapra grimmia*), Cape grysbok, Cape grey mongoose, domestic cat and steenbok. These were the only naturally occurring, or domestic, species of interest for which I had sufficient photographic captures. I used a subset of my data over a continuous 32-day period when all cameras were active (10 September to 11 October on the estate and 12 September to 13 October on the reserve). The mostly impenetrable fence between the estate and the reserve greatly reduces the possibility of animal movement between the two sites. In addition, there was considerable overlap in the timing of sampling periods, and hence probability of use estimates between the sites are comparable. I created a species detection/non-detection matrix for all species based on 8*4 day sampling occasions in order to increase the number of detections relative to non-detections. Because of the large number of Cape grysbok detections on the estate, I did not coalesce detections into smaller sampling periods, leaving the detection/no-detection matrix as 32*1 day sampling occasions for this species. Short occasions are optimal for species which are frequently detected, while longer occasions are better for species rarely detected (Winterton, Wilgen and Venter, 2020).

For each species I ran a global model, including all the covariates. I performed a goodness of fit test, on the global model using the *mb.gof.test* function in the R package *AICcmodavg* with 1000 bootstrapped samples (Mazerolle, 2020). I then used the *dredge* function in the R package *MuMIn* (Bartoń, 2020) to rank all possible models by AICc (Hurvich and Tsai, 1989). I used the highest-ranking model, unless the model did not converge, in subsequent probability of use modelling. I assessed model fit using the Pearson's chi-square p-value, with values greater than 0.1 reflecting acceptable model fit (MacKenzie and Bailey, 2004). The variance inflation factor (c-hat) is a measure of overdispersion (Burnham and Anderson, 2002). Values greater than one indicate overdispersion in a model, with values greater than four indicating lack of fit, while values far below one may indicate under dispersion in the model. I computed the variance inflation factor on the global model and confirmed each model was within under dispersion/overdispersion bounds (0.8<c-hat<1.4) (Burnham and Anderson, 2002). For each probability of use model, I back transformed both probability of use and detection estimates to convert estimates from the link scale to the original scale. I used the mean value of each covariate relevant to a particular model in back transforming.

I created extrapolated probability of use plots using the *predict* function in the R package *raster* (Hijmans, 2020). On the estate, human RAI was an informative covariate on the probability of use. I inputted human RAI at each station into Inverse Distance Weighted (IDW) Interpolation in QGIS v.3.8.0 (QGIS Development Team, 2019). I used this to predict human RAI for each 10 m pixel of natural habitat on the estate. NDVI was the only significant predictor of probability of use on the reserve. I extracted NDVI values at every pixel within the reserve outline, at a 10 m resolution, using the same satellite image as for probability of use/detection covariate, to get NDVI values at stations for probability of use modelling. I then used NDVI values for the coastal sector of the reserve and predicted human RAI values for the estate to create extrapolated probability of use plots.

Although there were two shared species between the estate and the reserve both with probability of use estimates, the estimates, though comparable, mean different things. It is important to contextualize probability of use estimates on the estate and the reserve. While I had a mirrored spatial configuration, including the same number of cameras on both sites (n=25), similar inter trap distance (220m on the estate and 225m on the reserve) and a similar number of trap nights (776 on the estate and 779 on the reserve), the effective trapping area was not the same. On the estate, species are excluded from residential housing, gardens and other estate facilities, while on the reserve all land between cameras is available for use by the species present. There is far more habitable land available within a minimum convex polygon encompassing all stations on the reserve compared to the estate. Considering this, I was careful not to use probability of use as a proxy for abundance.

Activity patterns

Antelope were the only guild which for which I had sufficient captures at both sites to analyse activity patterns. I detected four species of antelope on the camera array. Of these, three are indigenous with similar traits, while one, the springbok (*Antidorcas marsupialis*), in addition to being extralimital and thus introduced, differs in terms of body mass, group size and activity patterns (Table 4.3). Furthermore, I had few captures of grysbok on the nature reserve. I therefore decided to consider the combined activity of grysbok, duiker and steenbok on the nature reserve and of only grysbok on the estate.

Table 4.3: Characteristics of the antelope species found on Atlantic Beach Estate and Blaauwberg Nature Reserve[1].

Species	**Mass (kg)**	**Groups**	**Indigenous**	**Activity[2]**
Springbok	37-41	Large groups	No	Diurnal and nocturnal
Cape grysbok	10	Solitary	Yes	Nocturnal and crepuscular
Common duiker	18-21	Solitary or pairs	Yes	Crepuscular and nocturnal
Steenbok	11	Solitary or pairs	Yes	Crepuscular and nocturnal

[1]See Stuart and Stuart (2015).

[2]Activity listed first indicates primary activity period.

To investigate how the temporal activity of three antelope species varied between the two sites I extracted time-stamps from all independent captures of each species. These were used to create distributions of photographic captures across a 24-hour period (Ridout and Linkie, 2009). I calculated and subsequently compared activity level estimates (defined as the proportion of time animals spend active (Rowcliffe *et al.*, 2014)) using the R package *activity* (Rowcliffe, 2019). To account for differences in detection between day and night, I upweighted detections during the night (between sunset and sunrise) by 20 % (Rowcliffe, 2019). I calculated the coefficient of overlap (Δ) from these distributions of captures across a 24-hour period for both sites, using non-parametric calculations, as developed by Ridout and Linkie (2009). I utilized the Δ_4 estimator because the smallest sample was always greater than 50 captures (Ridout and Linkie, 2009). The coefficient of overlap can range from 0 to 1, where 1 represents complete overlap in temporal activity for both zones. Subsequent confidence intervals were calculated from 999 bootstrap samples. Temporal overlap was calculated using the R package *overlap* (Meredith and Ridout, 2020).

Results

Descriptive results

I conducted my camera trap survey over a total of 1555 camera trap nights (n=776 for the estate and n=779 for the reserve) with a total of 50 camera trap stations divided evenly across both sites. A total of 125 827 images were recorded, 104 497 of which were blank. Of the remaining 21 330 images, there were 6403 independent captures, 5146 of which were captures on the estate, while 1257 were captures on the reserve. The survey yielded 14 identifiable mammal species as well as various other small mammal, bird, insect and reptile species across both sites (Table 4.4).

Table 4.4: The number of independent captures of mammal species, other species and vehicles on Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR). Both the common name and the scientific name of species are provided.

Common name	Scientific name	ABE captures	BNR captures
African striped weasel	*Poecilogale albinucha*	2	1
Cape grey mongoose	*Galerella pulverulenta*	259	54
Cape grysbok	*Raphicerus melanotis*	506	48
Cape porcupine	*Hystrix africaeaustralis*	-	23
Caracal	*Caracal caracal*	-	4
Common duiker	*Sylvicapra grimmia*	-	238
Domestic cat[2]	*Felis catus*	304	-
Domestic dog[2]	*Canis lupus familiaris*	83	-
Domestic rabbit[2]	*Oryctolagus cuniculus*	8	-
Honey badger	*Mellivora capensis*	-	5
Small-spotted genet	*Genetta genetta*	8	29
Springbok[2]	*Antidorcas marsupialis*	391	-
Steenbok	*Raphicerus campestris*	-	54
Unknown antelope	-	2	20
Unknown	-	15	59
Human	*Homo sapiens*	1051	2
Research team	*Homo sapiens*	130	109
Vehicle	-	800	-
Other species			
Angulate tortoise	*Chersina angulata*	3	-
Bat spp.	-	1	1
Bird spp.	-	723	246
Gamebird[1]	-	846	198
Insect spp.	-	11	33
Rodent spp.	-	3	133

[1] Helmeted guineafowl (*Numida meleagris*), Cape spurfowl (*Pternistis capensis*) or Grey-winged francolin (*Scleroptila afra*).

[2] Non-native.

The highest number of captures on the estate was of humans, with vehicles and introduced species (namely domestic cats and springbok) also featuring prominently (Figure 4.2). The reserve had captures primarily of native species, with no introduced species and only a couple of human captures (Figure 4.2).

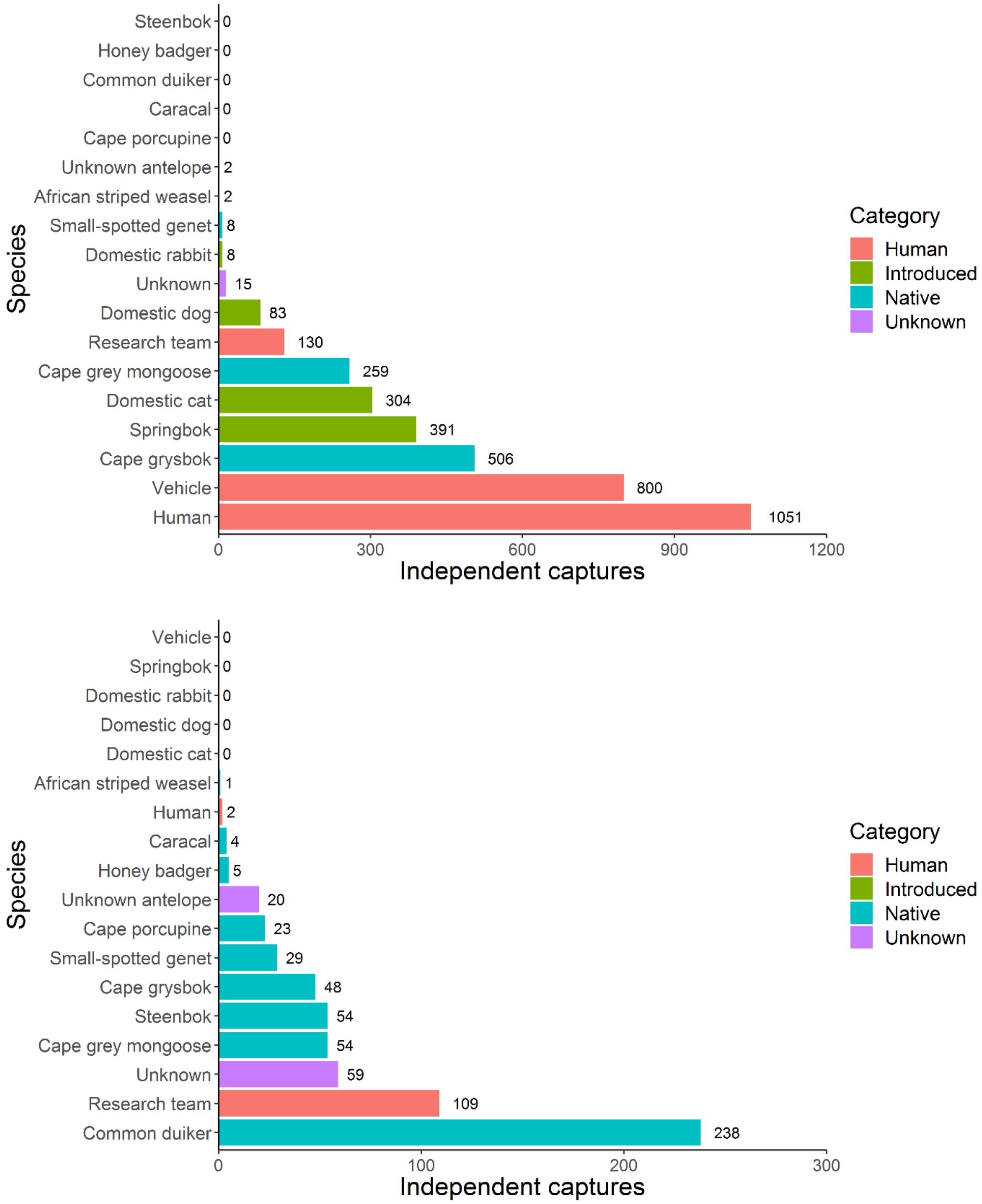


Figure 4.2: Number of independent captures of species coloured by category on Atlantic Beach Estate (top; n=4170; 776 trap nights) and Blaauwberg Nature Reserve (bottom; n=1176; 779 trap nights).

Rarefaction curves based only on target species indicate both sites were approaching asymptotes at eight and nine species for the estate and the reserve respectively and suggest that sufficient sampling had been performed (Figure 4.3).

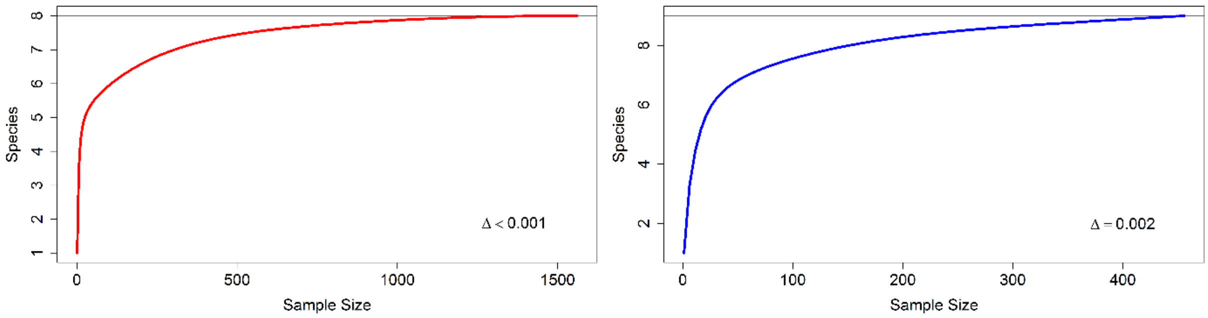
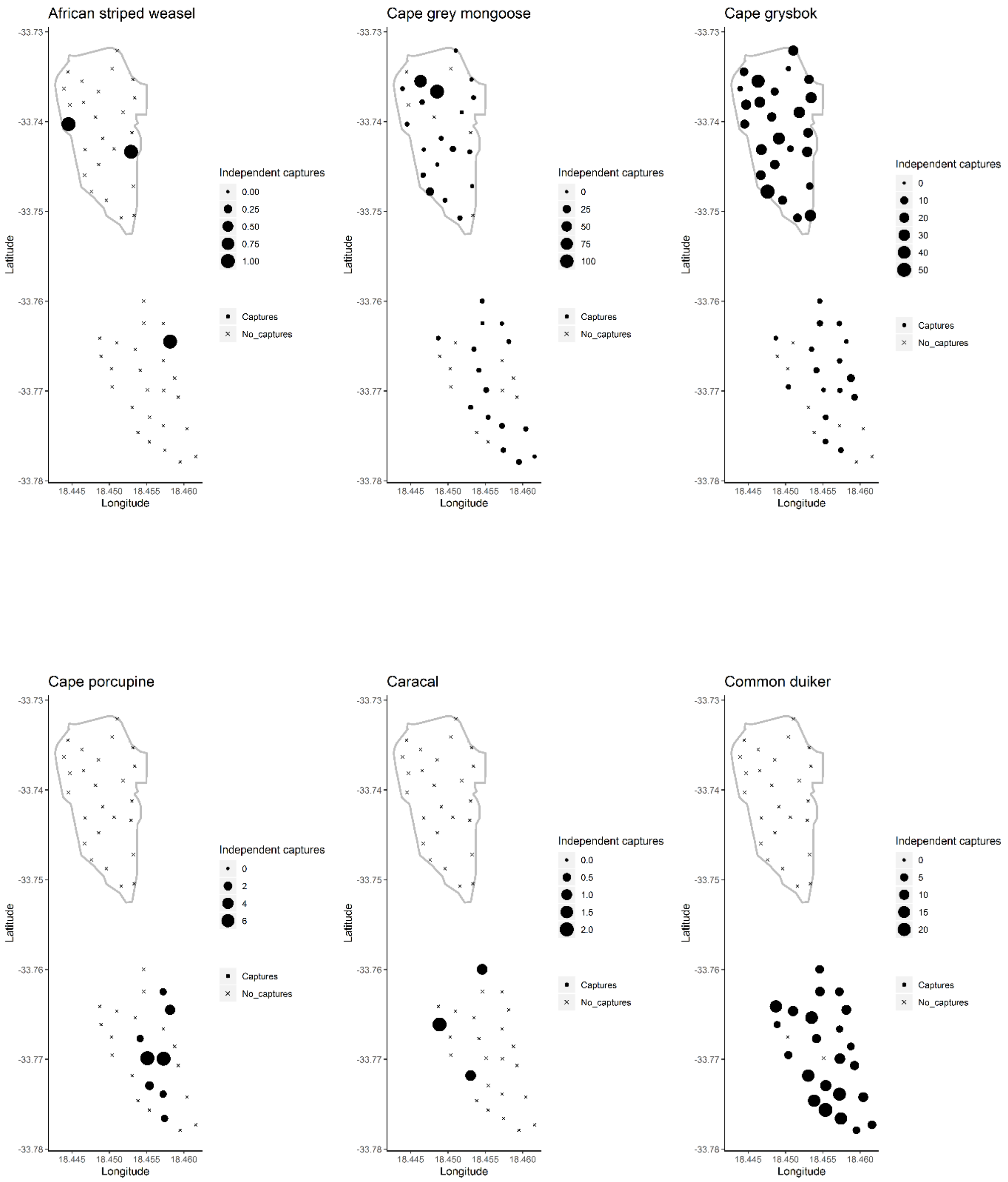
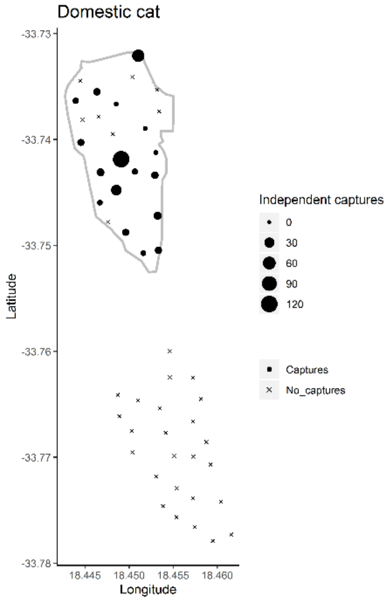
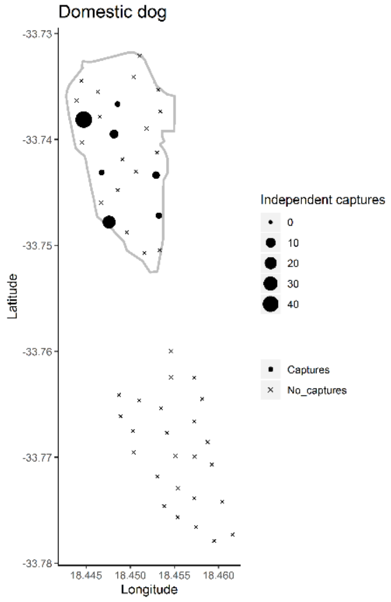


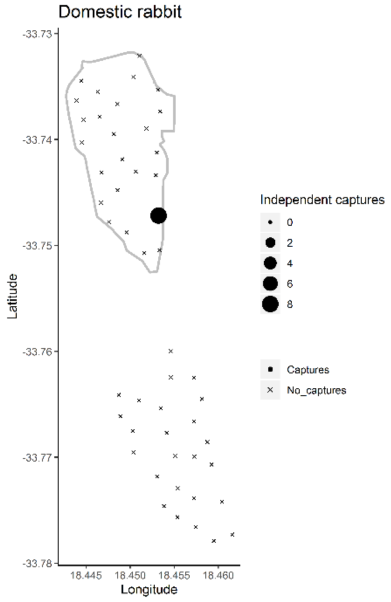
Figure 4.3: Site based rarefaction curve for Atlantic Beach Estate (left, in red) and Blaauwberg Nature Reserve (right, in blue). The delta symbol (Δ) indicates the gradient of the slope at the second-to-last sample, with low values indicating the curve is approaching an asymptote (ABE Δ<0.001, BNR Δ=0.002).

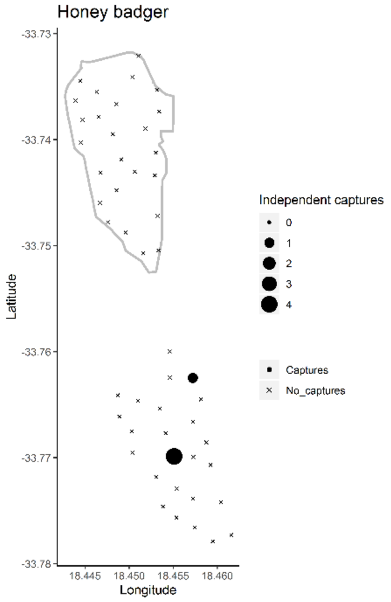
Independent captures were not evenly distributed among species, across sites or within sites (Figure 4.4). Cape grysbok (*Raphicerus melanotis*) were photographed at more stations than any other species, occurring at 41 of the 50 stations including all 25 stations on the estate and at 16 stations on the reserve. Domestic rabbit (*Oryctolagus cuniculus*) was the least widely occurring species, being photographed at only a single station on the estate. Domestic cat, domestic dog (*Canis lupus familiaris*), domestic rabbit, springbok and vehicle were photographed only on the estate, while Cape porcupine (Hystrix africaeaustralis), caracal, common duiker, honey badger (*Mellivora capensis*) and steenbok were photographed only on the reserve.

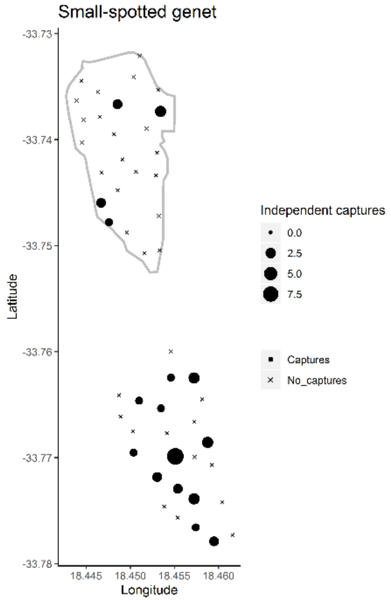

African striped weasel
Cape grey mongoose
Cape grysbok
Cape porcupine
Caracal
Common duiker
Latitude
Longitude
-33.73
-33.74
-33.75
-33.76
-33.77
-33.78
18.445
18.450
18.455
18.460
Independent captures
0.00
0.25
0.50
0.75
1.00
0
25
50
75
100
0
10
20
30
40
50
0
2
4
6
0.0
0.5
1.0
1.5
2.0
0
5
10
15
20
Captures
No_captures

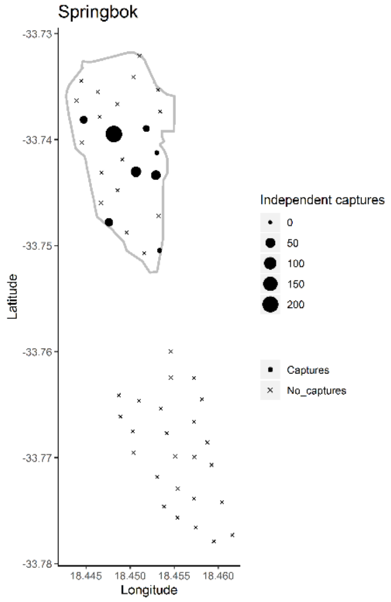

Domestic cat
Latitude
Longitude
-33.73
-33.74
-33.75
-33.76
-33.77
-33.78
18.445
18.450
18.455
18.460
Independent captures
0
30
60
90
120
Captures
No_captures


Domestic dog
Latitude
Longitude
-33.73
-33.74
-33.75
-33.76
-33.77
-33.78
18.445
18.450
18.455
18.460
Independent captures
0
10
20
30
40
Captures
No_captures


Domestic rabbit
Latitude
Longitude
-33.73
-33.74
-33.75
-33.76
-33.77
-33.78
18.445
18.450
18.455
18.460
Independent captures
0
2
4
6
8
Captures
No_captures


Honey badger
Latitude
Longitude
-33.73
-33.74
-33.75
-33.76
-33.77
-33.78
18.445
18.450
18.455
18.460
Independent captures
0
1
2
3
4
Captures
No_captures


Small-spotted genet
Latitude
Longitude
-33.73
-33.74
-33.75
-33.76
-33.77
-33.78
18.445
18.450
18.455
18.460
Independent captures
0.0
2.5
5.0
7.5
Captures
No_captures


Springbok
Latitude
Longitude
-33.73
-33.74
-33.75
-33.76
-33.77
-33.78
18.445
18.450
18.455
18.460
Independent captures
0
50
100
150
200
Captures
No_captures

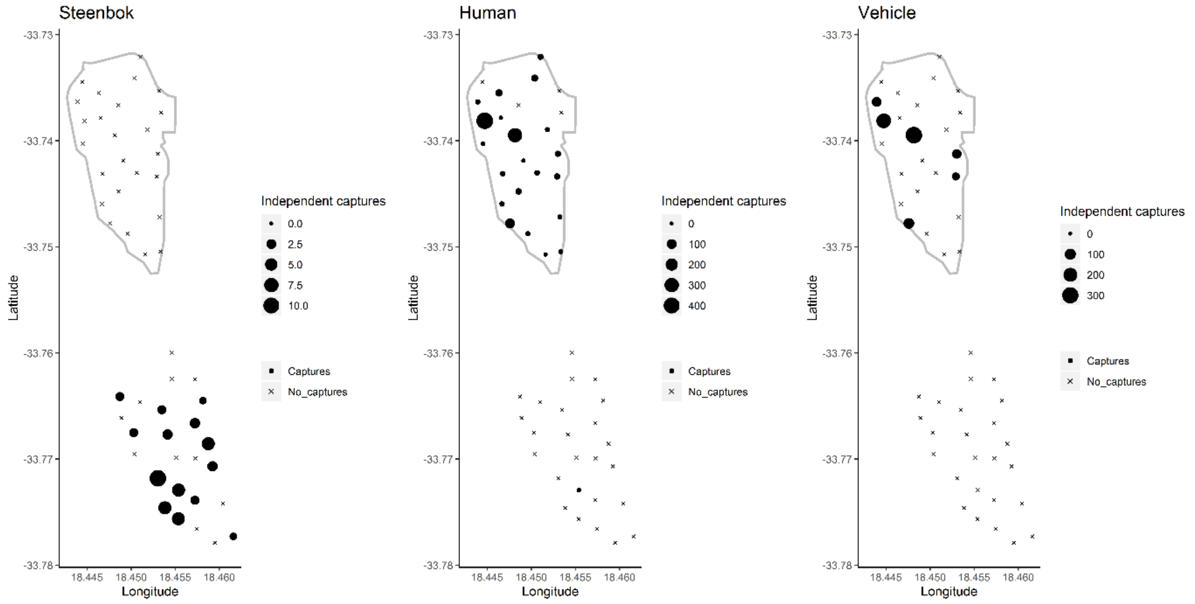


Figure 4.4: Distribution of independent captures of various species across Atlantic Beach Estate (upper cluster of points in each plot) and Blaauwberg Nature Reserve (lower cluster of points in each plot). The number of independent captures per station is denoted by the size of the circle, while stations with no captures are demarcated with an “x” (note that the scale is different for each species).

Relative abundance index (RAI)

Humans were the most active mammal on the estate (RAI=135.44), followed by Cape grysbok (RAI=65.21) and springbok (RAI=50.39) (Figure 4.5). In contrast, common duiker was the most active mammal in the reserve (RAI=30.55), followed by both Cape grey mongoose and steenbok (RAI=6.93) (Figure 4.5). Only African striped weasel (*Poecilogale albinucha)*, Cape grey mongoose, Cape grysbok, humans and small-spotted genet (*Genetta genetta*) occurred at both sites.

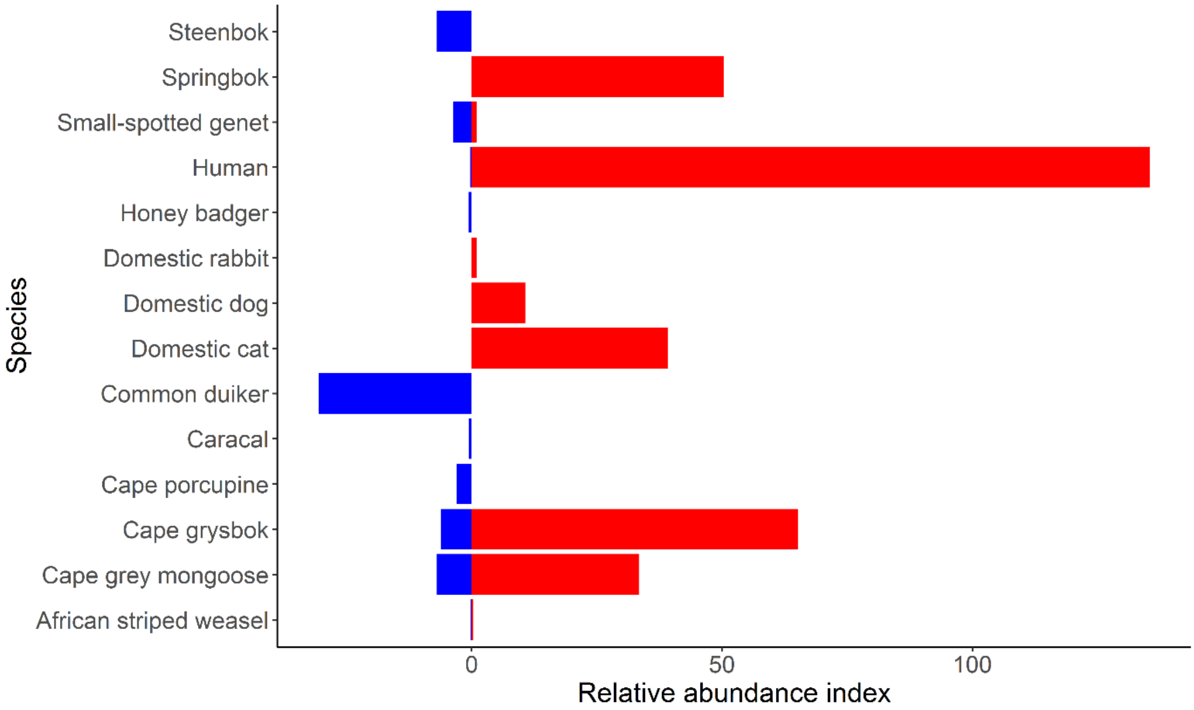


Figure 4.5: Relative abundance index (RAI) of various mammal species on Atlantic Beach Estate (right; in red) and Blaauwberg Nature Reserve (left; in blue)

Probability of use

I performed probability of use models only on species of interest, with sufficient captures (Table 4.5). Dredging global models for each of these species yielded the best fitting parameters for a probability of use model. For each species I used the best fitting model which converged and noted parameters for the null model for comparison (Table 4.5).

Table 4.5: Probability of use model parameters for the best fitting model and the null model. Probability of use models include parameters for detectability (ρ) and for probability of use (ψ). Included in the table are the degrees of freedom (df), corrected Akaike information criterion (AICc), difference in AICc (ΔAICc), AICc weight (AICcwt), the Pearson's chi-square p-value (chisq) and the variance inflation factor (c-hat). All species were pooled on 8*4 day sampling occasions, with the exception of Cape grysbok on Atlantic Beach Estate, which was left as 32 day unpooled sampling occasions.

	df	**AICc**	**ΔAICc**	**AICcwt**	**chisq**	**c-hat**
Common duiker BNR						
ρ(NDVI), ψ(1)	3	232.0	0.00	0.324	0.109	1.3
ρ(1), ψ(1)[1]	2	236.9	4.89	0.028		
Domestic cat ABE						
ρ(1), ψ(Human RAI)	3	213.4	0.00	0.425	0.228	1.13
ρ(1), ψ(1)	2	217.3	3.90	0.060		
Cape grysbok ABE						
ρ(NDVI), ψ(1)	3	1071.6	0.00	0.459	0.007	1.31
ρ(1), ψ(1)	2	1075.4	3.79	0.069		
Cape grysbok BNR						
ρ(1), ψ(NDVI)	3	170.7	0.70	0.124	0.369	0.90
ρ(1), ψ(1)	2	171.9	1.96	0.063		
Cape grey mongoose ABE						
ρ(NDVI), ψ(HumanRAI)	4	229.6	0.00	0.333	0.465	0.91
ρ(1), ψ(1)	2	234.1	4.45	0.036		
Cape grey mongoose BNR						
ρ(1), ψ(NDVI)	3	181.8	0.35	0.124	0.479	0.95
ρ(1), ψ(1)	2	183.9	2.52	0.042		
Steenbok BNR						
ρ(NDVI),ψ(NDVI)	3	161.9	0.936	0.121	0.918	0.83
ρ(1), ψ(1)	2	174.7	13.77	0.000		

[1] ρ(1), ψ(1) represents the null model.

I used the best fitting model for each species to create probability of use (Figure 4.6) and likelihood of detection (Figure 4.6) estimates on the estate and the reserve. Cape grysbok on the estate had the highest probability of use (ψ = 0.99±0.000094), while domestic cats had the lowest probability of use (ψ = 0.59±0.190). Common duiker had the highest probability of detection (ρ = 0.70±0.036), while Cape grysbok in the reserve had the lowest detection probability (ρ = 0.23±0.042).

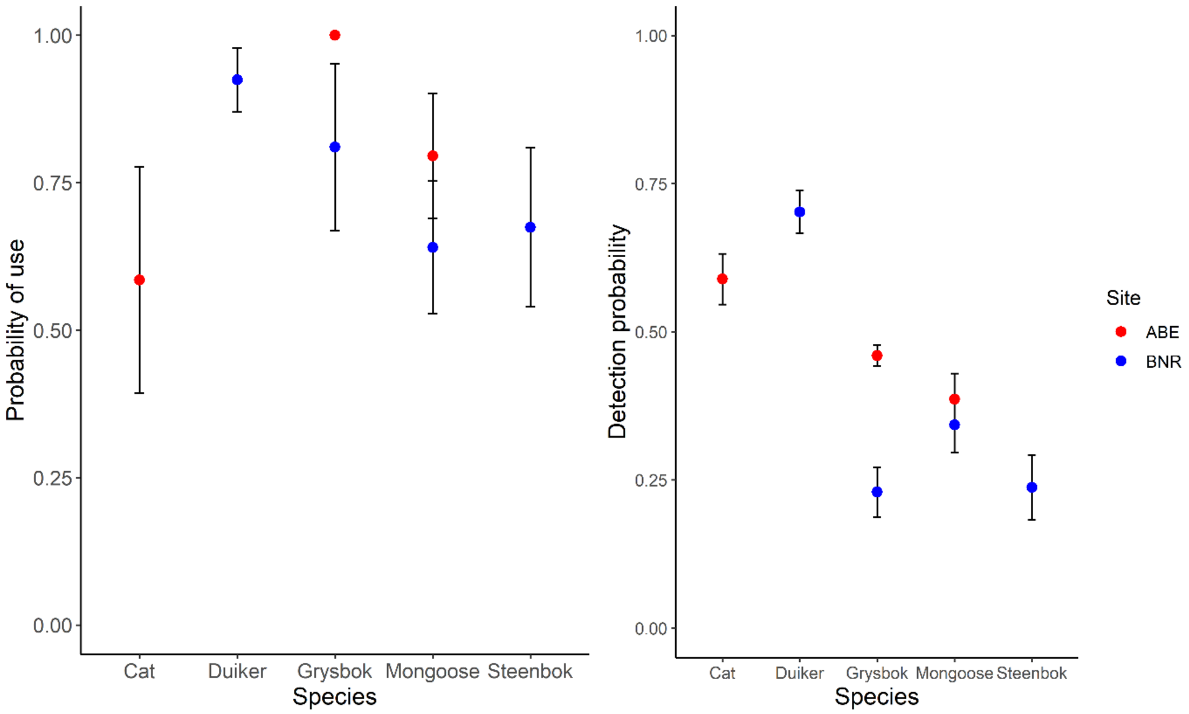


Figure 4.6: Probability of use (left) and detection probability (right) estimates for select species on Atlantic Beach Estate (ABE, shown in red) and Blaauwberg Nature Reserve (BNR, shown in blue). All species were modelled on pooled 4-day occupancy, except for Cape grysbok on the estate, which were left as unpooled 32-day observations.

Extrapolated probability of use estimates suggest*s* Cape grey mongoose and domestic cats utilise the estate similarly. Both species have a widespread predicted probability of use across the estate, except for a couple of sites in the centre and on the western border of the estate (Figure 4.7).

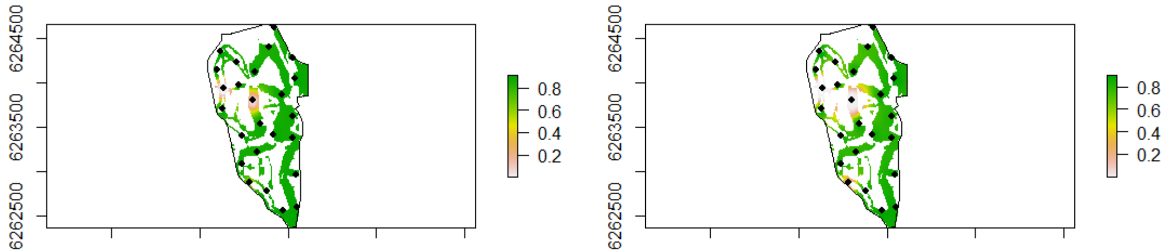


Figure 4.7: Extrapolated probability of use for Cape grey mongoose (left) and domestic cats (right) on Atlantic Beach Estate. These data are based on 8*4 day sampling periods, using no detection covariates and human relative abundance index as a probability of use covariate for both Cape grey mongoose and domestic cats. Black dots demarcate the positions of camera trap stations.

Both Cape grey mongoose and Cape grysbok probability of use on the reserve were positively correlated with NDVI and thus there was a high predicted probability of use to the north, where NDVI is higher (Figure 4.8).

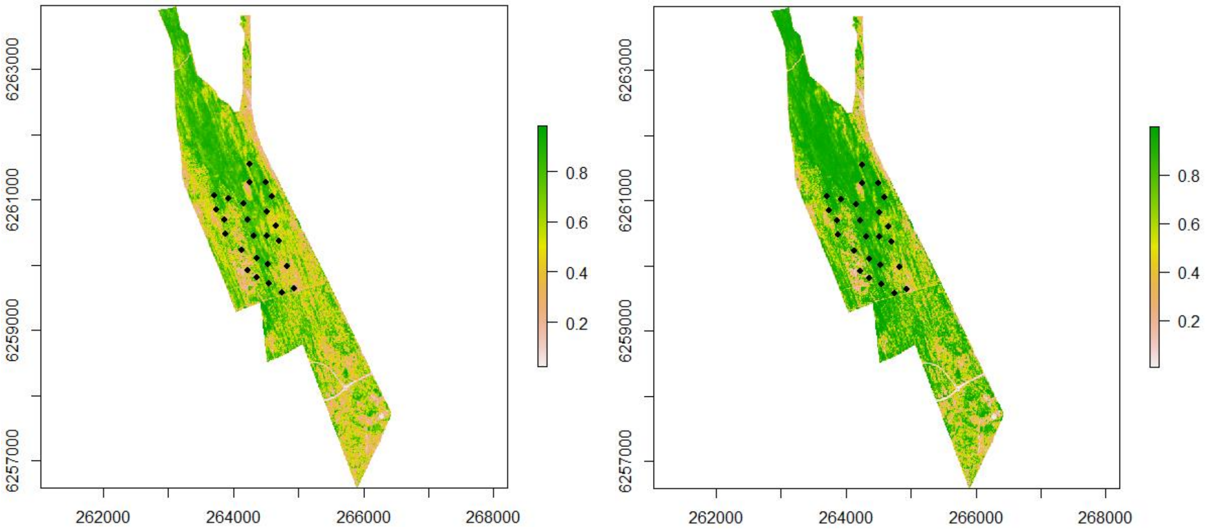


Figure 4.8: Extrapolated probability of use for Cape grey mongoose (left) and Cape grysbok (right) across Blaauwberg Nature Reserve. These data are based on 8*4 day sampling periods, using no detection covariates, and NDVI as a probability of use covariate. Black dots demarcate the positions of camera trap stations.

Steenbok probability of use on the reserve was inversely correlated with NDVI, such that steenbok were more likely to be found in areas of lower NDVI, and hence have a lower expected probability to the north, and a higher expected probability to the south (Figure 4.9).

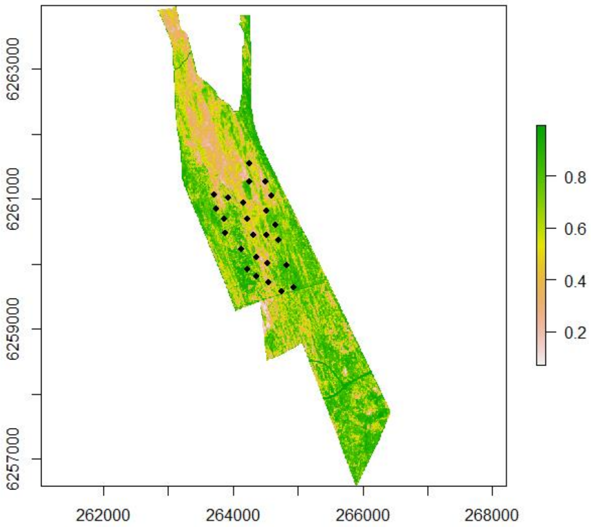


Figure 4.9: Extrapolated probability of use for steenbok across Blaauwberg Nature Reserve. These data are based on 8*4 day sampling periods, using no detection covariates, and NDVI as a probability of use covariate. Black dots demarcate the positions of camera trap stations.

Activity patterns

Cape grysbok on the estate and antelope on the reserve showed no difference in activity levels (Wald test for clock time W=0.003, p=0.96). Both populations were active for approximately half the day (Table 4.6).

Table 4.6: Activity level estimates of Cape grysbok on Atlantic Beach Estate (ABE) and antelope on Blaauwberg Nature Reserve (BNR), with associated standard error and a 95 percent confidence interval.

Site	Activity level	Standard error	Confidence interval
ABE	0.48	0.04	0.40 – 0.55
BNR	0.49	0.04	0.40 – 0.57

While there was no significant difference in the activity level of antelope between the estate and the reserve, there appeared to be temporal differences in when animals were active (Figure 4.10). Antelope on the estate were active primarily in the evening, between 19:00 and 05:00. In contrast, antelope on the reserve had peak activity in the early morning, between 06:00 and 10:00 and a second, lower peak just before 18:00. This represents a temporal shift in activity of antelope on the estate, resulting in an activity level overlap of 60 percent, despite almost identical activity level estimates.

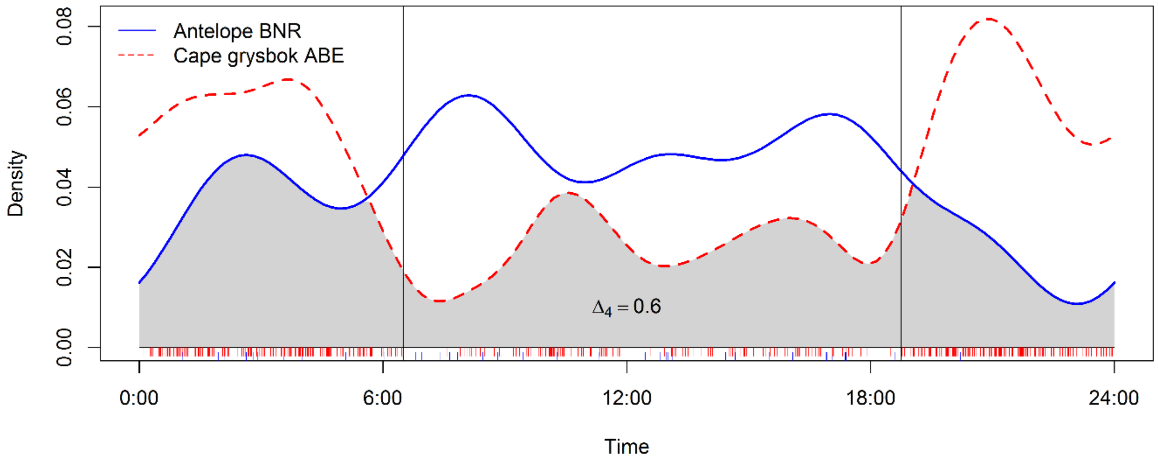


Figure 4.10: Activity pattern of Cape grysbok on Atlantic Beach Estate (red) and antelope (Cape grysbok, common duiker and steenbok) on Blaauwberg Nature Reserve (blue). The dotted red line represents the smoothed estimated activity for Cape grysbok on ABE, while the solid line represents the smoothed estimated activity for antelope on BNR. The lines along the bottom indicate the number of captures at each time interval. Δ_4 represents the overlap co-efficient.

Human activity and disturbance represent the major difference between conditions on the estate and those on the reserve. Overlap plots suggest increased human activity on the estate is associated with decreased Cape grysbok activity (Figure 4.11). This pattern was less clear on the reserve presumably because of a lower number of human captures (including research team) (Figure 4.11).

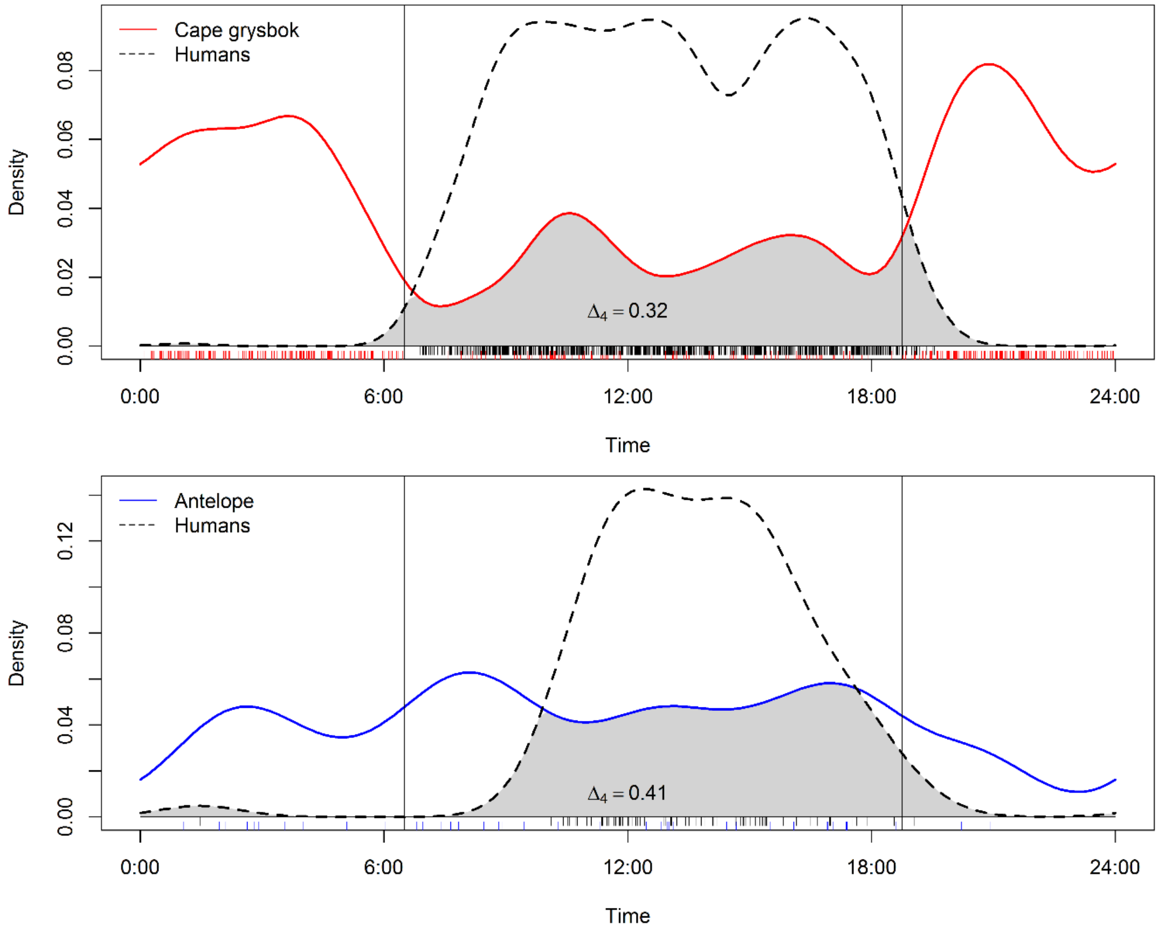


Figure 4.11: Activity pattern overlap for Cape grysbok and humans (including research team) on Atlantic Beach Estate (top) and all antelope (Cape grysbok, common duiker and steenbok) and humans (including research team) on Blaauwberg Nature Reserve (bottom). Δ_4 represents the overlap co-efficient.

Cape grey mongoose activity appears undisturbed by human activity, and as a result mongoose on both the estate and the reserve have similar activity patterns and a 90 % activity overlap (Figure 4.12).

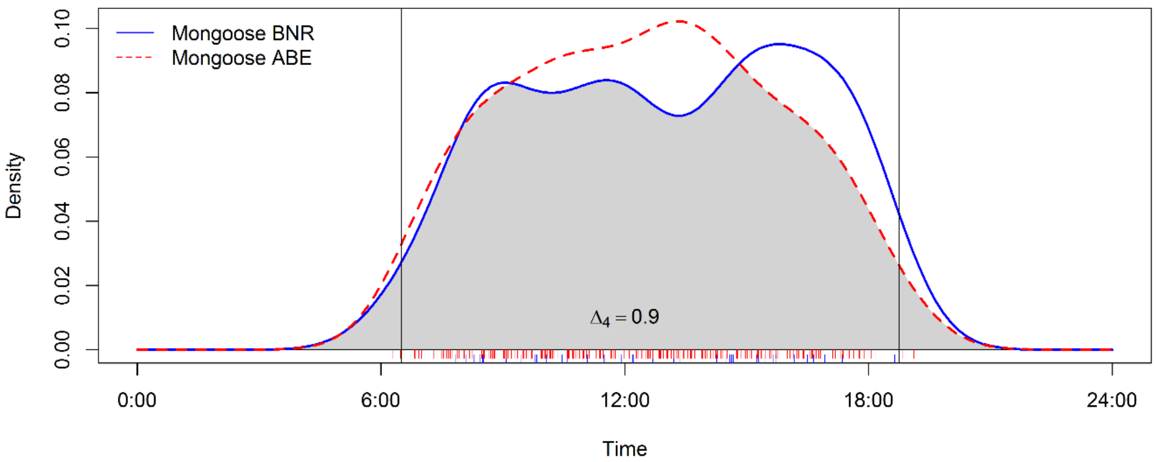


Figure 4.12: Activity pattern of small grey mongoose on Blaauwberg Nature Reserve (blue) and Atlantic Beach Estate (red). The solid line represents the smoothed estimated activity. The lines along the bottom indicate the number of captures at each time interval. Δ_4 represents the overlap co-efficient.

Discussion

The estate and reserve have a similar number of terrestrial medium-large mammal species, excluding humans (n=8 and n=9, respectively), however only four (50 %) of the species on the estate are native, compared to 100 % on the reserve. Of the non-native species on the estate, springbok and domestic dogs would not be able to penetrate the perimeter fence while both rabbits and cats could at select points. Encouragingly neither of the latter two introduced species were detected within the reserve despite the camera traps being well within the range of domestic cats moving from the estate (Wierzbowska *et al.*, 2012; Pillay, Streicher and Downs, 2018). This is an important finding for reserve management who were concerned about spill over of domestic species into the reserve, and in particular domestic cats which have been shown to exact a heavy toll on small wildlife in Cape Town (Loyd *et al.*, 2013; Seymour *et al.*, 2020) and urban areas globally (Loss, Will and Marra, 2013; Doherty *et al.*, 2016; Loss and Marra, 2017; Trouwborst, McCormack and Martínez Camacho, 2020).

The presence of introduced species on the estate was expected but not free ranging domestic animals within the public open spaces. This reveals that many residents do not observe the estate rules which demand that “all domestic animals are confined to private properties unless they are under the control of the owners and in the case of dogs, on a leash” (Atlantic Beach Homeowners Association, 2013). Free ranging domestic cats and dogs will have both non-lethal and lethal impacts on wildlife species and may influence the distribution, abundance and activity patterns of potential prey species in addition to similar sized competitors (Young *et al.*, 2011; Hughes and Macdonald, 2013; Doherty *et al.*, 2017; Trouwborst, McCormack and Martínez Camacho, 2020; Gompper, 2021).

Previous camera trap surveys on the estate and the reserve have yielded a similar suite of species to those recorded in this study. Cape grysbok, caracal, domestic cat, domestic dog, small-spotted genet and springbok have been previously recorded on camera traps in the estate (van Wyk, 2017). Similarly, in the reserve, Cape grey mongoose, Cape grysbok, Cape porcupine, caracal, common duiker, honey badger, small-spotted genet and steenbok were also previously recorded (van Wyk, 2017; Schnetler, 2019). However this is the first study to record African striped weasel in the study area and in greater Cape Town since a previous capture approximately 50 km away in the Helderberg Nature Reserve in 2013 (Schnetler, 2019). Together these two studies have added two new locations for the species in the South Western Cape (Child *et al.*, 2016).

Caracal have been seen regularly by residents within the estate (Nattrass and O'Riain, 2020) and recorded on both closed-circuit television footage linked to the estates security cameras and on camera traps placed opportunistically within the estate (L. Conradie, 2019, *pers. comm*.). Caracal are known to predate on domestic cats (Leighton *et al.*, 2020; Nattrass and O'Riain, 2020) with at least four confirmed predation events on the estate since 2013 (van Huyssteen, 2018) but many more suspected (around 66 (Nattrass and O'Riain, 2020)). I did not detect caracal within the estate but did record them in the neighbouring reserve. Caracal have previously been observed entering the estate through the main boomed entrances of the estate and leaving by jumping onto and then over the estate's electrified fence (see Appendix 4.2, Nattrass and O'Riain 2020). However, since 2019 caracal have rarely been detected within the estate and it is suspected therefore that much of this unusual behaviour, which culminated in a caracal killing a domestic cat within an occupied house, was attributed to a single caracal that has since died or emigrated.

Predicted species not detected

Striped polecat (*Ictonyx striatus*), which persists at low densities (0.1-0.2 / km²) throughout its range (Rowe-Rowe *et al.*, 2016), was detected in a recent survey of the whole reserve (Schnetler (2019)). It is possible that my more intensive sampling over a small effective area (1.7 km²) was unsuited to detecting this species. This survey also failed to detect Cape fox which were recorded (n=2 images) by van Wyk (2017)). Other species which were thought to still occur in the area but have not been recorded in any of the recent surveys include bat-eared fox (*Otocyon megalotis*) and black-backed jackal (*Lupulella mesomelas*). My results support the suggestion by Schnetler (2019) that both species are likely to have been locally extirpated with the occasional sightings possibly linked to dispersal events and not representative of a permanent, stable population.

Five native species (Cape porcupine, caracal, common duiker, honey badger and steenbok) were present in the reserve but absent from the estate. Given the proximity of the two sites this suggests that either these species avoid the estate, or they have been locally extirpated, and subsequent immigration prevented by the electrified perimeter fence. The small size of the estate (1.69 km^2, of which only 0.49 km^2 is natural vegetation) relative to the average home range of these species (0.39 km^2 for Cape porcupine (Ngcobo, Wilson and Downs, 2019), 26.9 km^2 for caracal (Avenant and Nel, 1998), 0.06 km^2 for common duiker (Furstenburg, 2018), up to 541 km^2 for honey badger in arid environments (Begg *et al.*, 2005) and 0.62 km^2 for steenbok (du Toit, 1993)) suggests only Cape porcupine and common duiker, both of which are known to persist in human modified landscapes (Birss, Relton and Selier, 2016; Palmer, Birss and du Toit, 2016), might have been able to persist within the estate once it was fenced. However, in the absence of immigration both species are unlikely to have been able to persist as a sustainable population. It is also possible that the introduction of an extralimital species (the springbok) may have resulted in the competitive exclusion of common duiker and steenbok, particularly in the fynbos (Birss, Relton and Selier, 2016; Palmer, Birss and du Toit, 2016).

The construction of a permeable fence between the estate and the reserve to improve the movement of both species (Birss, Relton and Selier, 2016; Palmer, Birss and du Toit, 2016) was in the initial conservation strategy for the estate. However, it seems likely that rising crime levels resulted in the upgrading of the perimeter fence to reduce permeability to humans and in the process restricted the movement of medium and large sized wildlife. An unintended positive outcome of reduced fence permeability is a restriction of domestic animal movement from the estate into the reserve. Given the well documented negative impacts of cats (Seymour *et al.*, 2020), dogs (Doherty *et al.*, 2017; Coronel-Arellano *et al.*, 2021) and rabbits (Parker, Burkepile and Hayt, 2006) on native fauna and flora this may have proven critical to conservation efforts within the reserve. While the original agreement for ceding land for the development of the estate required a permeable fence between the reserve and the estate, it may be argued that the current lack of permeability provides more advantages to the reserve than disadvantages to wildlife deprived of access to the heavily transformed estate.

Relative abundance indices

The distribution and relative abundance of species differed markedly across the two study sites with Cape grey mongoose being the most widely distributed (detected at the most camera stations) and having the highest RAI (33.38) within the estate. This is similar to previous camera trapping results on the estate (RAI=53.9, van Wyk, 2017) and suggests that this small and agile predator thrives within the mosaic of natural and transformed habitat within the estate. The distribution of Cape grey mongoose was far less even within the reserve with 72.6 % of captures obtained at just two stations and a much lower RAI (6.93). Cape grysbok also have a much higher relative abundance on the estate relative to the nature reserve and this too was similar to previous trends (van Wyk (2017)) and consistent with findings throughout Cape Town that this antelope thrives in disturbed habitats with adequate cover (Schnetler, Radloff and O'Riain, 2020). Cape porcupine and small-spotted genet displayed similar trends in my survey and that of van Wyk (2017), with low relative abundance indices at both sites. In contrast, common duiker and steenbok had much higher relative abundance within the reserve (>3x) than that reported by van Wyk (2017) but were absent from the estate for reasons discussed above.

van Wyk (2017) noted that domestic cats were the most active mammal on the estate, followed by domestic dogs (combining dogs under control and uncontrolled), while I found that domestic cats were the fourth most active mammal, almost four times more active than domestic dogs. This suggests that dog owners might be taking more responsibility and keeping their pets on their property in accordance with the estate rules, but there is still a high domestic cat RAI which presents a threat to small mammals and birds on the estate.

Probability of use

Both domestic cats and Cape grey mongoose probability of use decreased with increasing human RAI. Humans were mostly detected on the cameras facing the golf course, which were characterized by open spaces with little cover that make such areas unsuitable for both domestic cats and Cape grey mongoose, both of which prefer concealment from larger predators (e.g., raptors) and closed habitats in which to hunt small prey (Doherty, Bengsen and Davis, 2014; Stuart and Stuart, 2015).

NDVI was a significant predictor of probability of use for three of the four species considered in the reserve. For Cape grey mongoose and Cape grysbok, probability of use increased with increasing NDVI, however for steenbok, the probability of use decreased with increasing NDVI. These results are consistent with species characteristics, as Cape grysbok require cover (Stuart and Stuart, 2015; Palmer *et al.*, 2016) while steenbok prefer open habitat with some cover (Stuart and Stuart, 2015). Cape grey mongoose have a wide range of habitat tolerances, however they are often located near refuge areas and away from open fields where they are vulnerable to predation (Stuart and Stuart, 2015; Do Linh San *et al.*, 2016). As Cape grey mongoose activity patterns indicated, mongoose had similar activity patterns across both sites, potentially because mongoose were buffered by human disturbance because of their propensity to seek out vegetation cover. Distance to roads was not an important variable for species probability of use on the reserve, possibly because the camera traps were all at least 190m from the nearest road, separated by dense vegetation, which has been shown to limit the influence of edge effects (Saunders, Hobbs and Margules, 1991).

Activity patterns

Grysbok on the estate showed a marked shift towards nocturnality relative to antelope within the reserve. Humans on the estate were primarily active during the day, between sunrise and sunset, while grysbok were primarily active in the night, in contrast to antelope on the reserve, which were slightly more active in the day than the night. Grysbok are an adaptable species which persist well within human-modified landscapes (Palmer *et al.*, 2016) but they typically avoid peaks of human activity. A shift to a greater degree of nocturnality may have costs, such as decreased foraging opportunities and increased metabolic costs and difficulty navigating (Sih, 2013). However, these costs may be offset by conditions within the estate including reduced predation risk from natural predators, higher nutrient value of plants that are routinely watered and fertilized on the estate and access to abundant water supplies. I observed minimal human disturbance on the nature reserve during my study, but reserve management has previously noted the presence of vagrants (Retief, 2019). Humans are not permitted to enter the coastal sector of the reserve without permission from reserve management, and even then are allowed only on the designated hiking trail. Thus the higher activity of antelope within the reserve during daylight hours likely reflects the reduced levels of human activity.

Conclusions, limitations and recommendations

Though the estate and the reserve have a similar number of medium-large mammal species (excluding humans) (n=8 and n=9), only four on the estate are native, compared to nine on the reserve. The intensive camera trapping array I set up in the estate allows for a high level of confidence about the species richness of mammals on the estate but cannot be considered a comprehensive survey of the reserve because of the limited coverage of what is a much larger area. This is likely to have reduced the detection probability of some species such as striped polecat which occur at very low densities and those that prefer high lying terrain as is typical of the southeastern portion of the reserve (e.g., rock hyrax (*Procavia capensis*)). Additionally, the design of the camera trapping array made some co-variates (e.g., distance to roads) unsuitable for probability of use modelling as there was too little variation in these variables.

Despite the limited extent of the array in the reserve I recorded Cape porcupine, caracal, common duiker, honey badger and steenbok none of which were found in the estate. Species richness on the estate is bolstered by the presence of domestic cats, domestic dogs and domestic rabbits and the introduction of an extralimital species, the springbok. Thus, while eco-estates offer suitable habitat for the persistence of select wildlife species they are also associated with the disruption of natural systems through the introduction of exotic species, some of which have significant negative impacts on other native fauna (Vitousek *et al.*, 1997; Gaertner *et al.*, 2016; van Wilgen *et al.*, 2020). Native species residing within the estate may adjust to the presence of humans through a shift in their activity patterns as evidenced by more nocturnal activity for Cape grysbok. However smaller species such as

Cape grey mongoose may use the cover provided by dense patches of natural and exotic vegetation on the estate to avoid detection while being active.

While the fence between the reserve and the estate is largely impenetrable to most mammals in the area and thus a clear violation of the agreement with the provincial and local conservation authorities (that the estate needs to ensure that animals can move from the reserve in the south to the natural land to the north of the estate), it may nevertheless be in the best interests of local fauna in the reserve. I did not detect any domestic animals in the reserve and this may be because of the difficulties of negotiating the electrified fence with a small mesh size and the risk of predation by caracal (Leighton *et al.*, 2020; Nattrass and O'Riain, 2020). Altering the fence to make it more permeable to wildlife may result in more homogeneous and connected mammal communities between the two sites but comes with high risks associated with domestic animals moving into the reserve. On balance I would argue that protecting the integrity of the reserve through limiting the ingress of domestic species by the presence of a well-maintained impenetrable fence has more conservation value than attempting to reinstate the estate as a movement corridor to allow wildlife to move north and south. Furthermore, the dense road network within the estate poses a risk to wildlife moving through the area as does the presence of domestic dogs that are not under control of their owners. Consequently, species such as grysbok which are together with springbok "locked in" to the estate need to be managed as part of a metapopulation to ensure some genetic mixing with other isolated populations in the greater Cape Town region (Hanski and Simberloff, 1997; Watson and Chadwick, 2007; Davies-Mostert, Mills and Macdonald, 2015). To the best of my knowledge both species are actively being managed in this way and I would support a continuation of this process to ensure the genetic health of species that can adapt to isolated human impacted areas.

The high level of domestic cat activity on the estate is a concern given the devastating impact cats can have on the local fauna. Estate management should enforce internal estate rules, insisting that domestic cats are confined to their respective owners' property. Some residents have taken the initiative by building catios, which enclose their garden or portions of thereof, preventing both the intrusion of caracal and the extrusion of cats onto public open spaces on the estate (Nattrass and O'Riain, 2020; Cecchetti, Crowley and McDonald, 2021). All domestic cats on the estate should be made to wear bells, which are effective in reducing domestic cat foraging success on native fauna (Nelson, Evans and Bradbury, 2005; Willson, Okunlola and Novak, 2015; Cecchetti, Crowley and McDonald, 2021). Should cats be found roaming about the estate they should be photographed and their owners fined.

Appendix 4.1 Relative abundance indices of mammals

Table S4.1.1: Relative abundance indices for mammal species detected on Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR).

Species	ABE	BNR
African striped weasel	0.26	0.13
Cape grey mongoose	33.38	6.93
Cape grysbok	65.21	6.16
Cape porcupine	-	2.95
Caracal	-	0.51
Common duiker	-	30.55
Domestic cat	39.18	-
Domestic dog	10.7	-
Domestic rabbit	1.03	-
Honey badger	-	0.64
Human	135.44	0.26
Small-spotted genet	1.03	3.72
Springbok	50.39	-
Steenbok	-	6.93

Table S4.1.2: Relative abundance indices for mammal species on Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR). Data are from a camera trapping survey conducted on both sites by van Wyk (2017).

Species	ABE	BNR
African striped weasel	-	-
Cape grey mongoose	53.9	42.8
Cape fox (*Vulpes chama*)	-	0.4
Cape grysbok	34.8	7.5
Cape porcupine	-	1.5
Caracal	-	-
Common duiker	-	9.8
Domestic cat	80.5	-
Domestic dog	64.6	-
Domestic rabbit	-	-
Honey badger	-	-
Human	-	-
Small-spotted genet	3.4	1.5
Springbok	50.5	-
Steenbok	-	1.9

Appendix 4.2 Photographic captures of species of interest

Figure S4.2.1: Security camera footage showing a caracal scaling the electric fence surrounding Atlantic Beach Estate (Nattrass and O'Riain, 2020).

Figure S4.2.2: Photographic capture of an African striped weasel on Atlantic Beach Estate taken by one of my camera traps.

Appendix 4.3 Probability of use model covariates

Table S4.3.1: Probability of use model covariates.

Station	X	Y	Site	NDVI	Disttoroads	HumanRAI	Camera
1	18.45104	-33.7321	ABE	0.501971	-0.99043	-0.04317	16MP
2	18.45039	-33.73409	ABE	0.696102	-0.82646	0.117936	16MP
3	18.45316	-33.7353	ABE	0.22807	-0.95624	-0.27649	16MP
4	18.45342	-33.73734	ABE	0.677096	-0.98465	-0.28946	16MP
5	18.44452	-33.74028	ABE	0.724894	-0.72422	-0.25057	16MP
6	18.44472	-33.73813	ABE	0.778145	-0.79931	5.53069	16MP
7	18.44444	-33.73445	ABE	0.689269	-0.91083	-0.27649	16MP
8	18.44392	-33.73633	ABE	0.843503	-0.83463	-0.19872	12MP
9	18.44854	-33.73665	ABE	0.537835	-0.85676	-0.26353	12MP
10	18.44633	-33.7355	ABE	0.517826	-0.87457	0.151269	12MP
11	18.45303	-33.74123	ABE	0.534857	-0.88454	-0.08206	16MP
12	18.45293	-33.74337	ABE	0.474176	-0.96901	-0.04317	12MP
13	18.45065	-33.74303	ABE	0.297968	-0.83207	-0.14687	12MP
14	18.4491	-33.74187	ABE	0.508636	-0.93441	-0.22464	12MP
15	18.44816	-33.73948	ABE	0.481923	-0.7214	3.767795	16MP
16	18.44676	-33.7431	ABE	0.343241	-0.97598	-0.17279	12MP
17	18.45184	-33.73896	ABE	0.690141	-0.76392	-0.18576	16MP
18	18.45323	-33.74719	ABE	0.823988	-0.93201	-0.22464	16MP
19	18.45333	-33.75045	ABE	0.547357	-0.9765	-0.25057	12MP
20	18.4516	-33.75073	ABE	0.579922	-1.00654	-0.27749	12MP
21	18.4496	-33.74876	ABE	0.606818	-0.86528	-0.19047	16MP
22	18.44857	-33.74478	ABE	0.68709	-0.83963	0.019971	16MP
23	18.44669	-33.74596	ABE	0.675587	-0.80321	-0.18074	12MP
24	18.4476	-33.74779	ABE	0.563833	-0.66731	1.170703	12MP
25	18.44654	-33.73784	ABE	0.517612	-0.95091	-0.22088	16MP
1	18.45743	-33.77658	BNR	0.642162	1.613269	-0.22818	12MP
2	18.45949	-33.77789	BNR	0.705977	1.902964	-0.2744	16MP
3	18.46159	-33.77729	BNR	0.389671	1.053934	-0.24913	16MP
4	18.46043	-33.77422	BNR	0.482745	0.864566	-0.27749	16MP
5	18.45384	-33.77461	BNR	0.262136	0.616065	-0.27649	16MP
6	18.45723	-33.77387	BNR	0.555629	1.914216	-0.26811	16MP
7	18.45538	-33.77292	BNR	0.520627	1.441903	-0.27217	16MP
8	18.45537	-33.77564	BNR	0.395966	1.012108	-0.26811	16MP
9	18.45305	-33.77181	BNR	0.359361	0.787285	-0.26353	16MP
10	18.45414	-33.76769	BNR	0.615324	1.796357	-0.28205	12MP
11	18.45924	-33.77069	BNR	0.596821	0.5903	-0.26811	16MP
12	18.45348	-33.76535	BNR	0.608061	1.566058	-0.28031	12MP
13	18.45876	-33.76856	BNR	0.444983	0.344747	-0.30471	12MP
14	18.4546	-33.75998	BNR	0.667205	0.130255	-0.30471	12MP
15	18.45512	-33.76988	BNR	0.627974	1.850989	-0.30471	16MP
16	18.45815	-33.7645	BNR	0.498513	-0.2312	-0.29251	16MP
17	18.45725	-33.76663	BNR	0.508267	0.497423	-0.28946	12MP
18	18.45461	-33.76245	BNR	0.663098	0.606158	-0.28031	12MP
19	18.45723	-33.76248	BNR	0.608208	-0.3027	-0.29251	16MP

20	18.44888	-33.76612	BNR	0.500909	0.232044	-0.28049	8MP
21	18.44872	-33.76411	BNR	0.537102	0.507355	-0.28049	8MP
22	18.45101	-33.76462	BNR	0.510585	1.246542	-0.28049	8MP
23	18.45728	-33.76993	BNR	0.483229	1.130287	-0.28049	8MP
24	18.45039	-33.76953	BNR	0.540282	0.208524	-0.28049	8MP
25	18.45028	-33.76751	BNR	0.495707	0.501358	-0.28049	8MP

CHAPTER 5: Birds

Abstract

Birds are the most well studied group of terrestrial vertebrates on the planet and perform many critical roles in an ecosystem. Additionally, birds are highly species diverse and widespread, making them useful as an indicator taxon. Using point counts and call playbacks I compared bird communities on Atlantic Beach Estate, a high security golfing eco-estate situated 30 km north of Cape Town, on South Africa's West Coast, with those in the neighbouring Blaauwberg Nature Reserve. I performed 120 point counts at 20 sites in the estate and 20 sites in the reserve in November 2019. After a 10-minute observation period I shuffled through 16 calls of inconspicuous but responsive taxa and recorded responses. Results indicate a significant difference in bird communities, with a higher species richness, Shannon-Wiener diversity and Pielou's evenness of birds on the estate compared to the reserve. In addition to supporting most species found in the reserve, the estate hosted a multitude of fynbos native species, urban exploiting species and water birds. Dissimilarity matrices, cluster analysis and Non-metric Multi-dimensional Scaling revealed larger between, than within, site variation. The presence of water and distance to nature reserve were significant predictors of species richness on the estate, explaining 58 % of the variance. These findings suggest that residential golf eco-estates that include a diverse mosaic of habitat types and associated resources have the potential to support more species than the surrounding natural habitat. Urban areas can support considerable avian diversity suggesting this taxon may typically do better than less vagile taxa which are more directly impacted by anthropogenic impacts.

Introduction

Birds are an important component of both natural and human-dominated ecosystems (Şekercioğlu, 2006; Whelan, Şekercioğlu and Wenny, 2015; Michel, Whelan and Verutes, 2020) occupying a broad range of niches (MacArthur and MacArthur, 1961; Whelan, Wenny and Marquis, 2008) and acting as mobile links, connecting geographically isolated areas and thereby enhancing ecosystem resilience (Lundberg and Moberg, 2003; Garcia, Zamora and Amico, 2010; García *et al.*, 2013; González-Varo *et al.*, 2017). The City of Cape Town is home to an estimated 367 indigenous bird species, which perform many important functions (Şekercioğlu, 2006; Whelan, Wenny and Marquis, 2008; Holmes *et al.*, 2012; Whelan, Şekercioğlu and Wenny, 2015). One of the more widely recognized functions of birds in the city, and in the Cape Floristic Region (CFR) generally, are their role as pollinators, with approximately 4 % of all flowers, in the most diverse floral kingdom in the world by area, reliant upon birds for pollination (Rebelo, 1987; Simmons and Cowling, 1996). Despite their importance, bird species in Cape Town are threatened by habitat destruction and degradation, invasive species, disease, climate change and extreme climatic events (Rebelo *et al.*, 2011; Turner, 2017; Coetzee, Barnard and Pauw, 2018). The expanding human footprint has forced natural habitat into small geographically isolated natural reserves which vary in suitability for birds (Taylor and Peacock, 2018). Non-native invasive bird species threaten local birds by hybridization, direct competition, or detrimentally altering the environment (Turner, 2017). At least eight exotic bird species (including common starling (*Sturnus vulgaris*) and house sparrow (*Passer domesticus))* have established free ranging populations within the Western Cape province and threaten the local biodiversity, while at least 18 indigenous species have colonized the province since the 1940s (Hockey, Dean and Ryan, 2005; Hockey and Midgley, 2009).

Considering the importance of birds to an ecosystem and given increased levels of urbanisation, it is worth considering the impact of urbanisation on bird communities. In general, moving from a rural to an urban landscape, bird communities become simpler, with fewer species and a higher prevalence of omnivores, granivores and cavity nesting species (Chace and Walsh, 2006; Reis, López-Iborra and Pinheiro, 2012; Aronson *et al.*, 2014). Select raptors may also increase in prevalence given the abundant food supply and if they are protected from persecution (Kettel *et al.*, 2018; McPherson, Sumasgutner and Downs, 2021). While species richness often decreases, there may be an increase in total biomass in urban areas (Chace and Walsh, 2006). Bird communities in urban areas may show a reduced functional diversity of up to 20 % when compared to surrounding natural land (Sol *et al.*, 2020). Bird species can be characterised as urban exploiters, urban tolerators, or urban avoiders, depending on their capacity to persist and indeed thrive in urban areas (Blair, 1996). On a finer scale, it is important to recognize that urban areas are a mosaic of natural patches and highly human modified structures and spaces, which vary greatly in suitability both for birds generally, and for some species specifically (Alexander *et al.*, 2019a, 2019b; Maseko *et al.*, 2019). Bird communities vary across the urban mosaic, with core areas containing primarily generalist, urban exploiters, while the periphery and large, well-connected patches can retain a multitude of native species (Chace and Walsh, 2006; Aronson *et al.*, 2014).

Bird communities on eco-estates are likely to be shaped by the conditions on the specific estate. Eco-estates which retain large, well-connected patches of natural vegetation are likely to retain many native bird species, including habitat specialists, particularly if these patches are connected to surrounding natural land (Alexander *et al.*, 2019a, 2019c). Species richness can be further bolstered by the inclusion/construction of water bodies, which facilitates the presence of obligate water users and bird feeders, which can encourage nectar-feeding specialists (Suri *et al.*, 2017; Coetzee, Barnard and Pauw, 2018). An eco-estate may function as an intermediately disturbed habitat, which can support both urban species and rural species, and hence may have a higher species richness than surrounding natural land (Roxburgh, Shea and Bastow Wison, 2004). However, in cases where natural land is replaced by large swathes of uniform cover (e.g., a golf course), bird communities may be simplified, with an increased prevalence of urban exploiting species, and fewer habitat specialists (Blair, 1996).

Birds are relatively easy to study because they display a large variation in morphology, plumage, behaviour and vocalizations which makes them easily identifiable to species level (Sullivan *et al.*, 2009; Troudet *et al.*, 2017). Many bird species are also highly visible, or generally detectable (Chace and Walsh, 2006; Gardner *et al.*, 2008). Consequently, birds are the most well studied group of terrestrial vertebrates on the planet (Şekercioğlu, 2006) and commonly used as an indicator taxon for ecological impact studies (Hilty and Merenlender, 2000; Sullivan *et al.*, 2009). Indicator taxa, by definition, can be used to make inferences about environmental performance and are thus useful for comparing anthropogenic impacts either within a before and after design or a comparison between a disturbed and undisturbed site(s) (Landres, Verner and Thomas, 1988; O'Connell, Jackson and Brooks, 2000; Browder, Johnson and Ball, 2002; Larsen, Sorace and Mancini, 2010; Kampichler *et al.*, 2014; Doyle, Gray and McMahon, 2020).

Avian abundance and diversity was previously (in 2005) compared between the northern half of the Atlantic Beach Estate (completed in 2002) and Blaauwberg Nature Reserve, prior to the completion of the estate (Fox and Hockey, 2007). Given the recent changes in land use, the bird communities were almost certainly not at equilibrium at the time of sampling, defined as the point when immigration matches emigration, and also referred to as the "relaxation time" (i.e., time to equilibrium) (Diamond, 1972). It is possible that certain species may have been declining rapidly at the time of sampling and have since become locally extinct (Lande, 1988). Additionally, urban exploiters may not have had sufficient time to colonize the estate and the vegetation that attracts many birds within urban areas may not yet have matured to the stage of flowering and fruiting. Utilizing some of the same sites, with the same census methods could allow for a better understanding of bird communities at equilibrium and provide a more holistic view on the status and trajectories of bird populations in human modified landscapes relative to natural areas.

Rational, aims and predictions

Native bird species within Cape Town and around the world are under threat from anthropogenic impacts and this is almost certainly going to increase as the human population continues to expand (Pimm *et al.*, 2006). Eco-estates are likely to become increasingly prevalent, with mounting pressure to develop housing on previously undeveloped sites. It is therefore crucial to quantify the impacts such developments have on bird diversity and the extent to which birds can persist in human-modified land. In this chapter I aim to extend the efforts of Fox and Hockey (2007) to assess how bird communities within both the estate and the neighbouring reserve have changed over time relative to each other. I predicted that larger, more contiguous habitats would support more native species and therefore that the estate will support fewer species that depend on natural vegetation than the reserve (MacArthur and Wilson, 1967; Martensen, Pimentel and Metzger, 2008). Furthermore I expect that bigger patches of natural habitat on the estate, and patches closer to the reserve, will support more species than smaller patches, or those near the centre of the estate (Ehlers Smith *et al.*, 2018; Amaya-Espinel *et al.*, 2019; Maseko *et al.*, 2020). However, the estate is likely to support a higher number of urban exploiting species (including water birds) because of the increased availability of food, shelter, artificial water sources and habitat diversity.

Methods

Monitoring bird species can be done in a number of different ways (e.g., point counts, line transects and mist netting), each subject to inherent flaws, but all being valuable when used correctly in appropriate circumstances (Bibby, Burgess and Hill, 1992). Point counts are a commonly used technique and are widely suitable for monitoring, particularly in areas which are difficult to navigate and thus preclude using line transects (Sutherland, 2006). Point counts can be used in conjunction with other counting techniques including vocalisation playbacks (Sutherland, 2006). Point counts do not necessarily seek to estimate species abundance and can successfully monitor changes in populations without deriving abundance estimates for a particular species. Thus the Southern African Bird Atlas Project (SABAP), utilises only presence/absence data and relative reporting rates to monitor changes in the distribution of species across southern Africa (Underhill, Brooks and Loftie-Eaton, 2017). Repeating these surveys allows one to make inferences about population changes and possible environmental impacts using select indicator species.

Data collection

The impenetrable, thicket-like nature of the natural vegetation in the area prevented walking transects and thus I used point counts (Bibby, Burgess and Hill, 1992) similar to Fox and Hockey (2007). I used the same spatial configuration of point count locations (interchangeably referred to as sampling sites) on the reserve as on the estate (Figure 5.1). Because of the limited number of patches of natural habitat on the estate, I designed my survey on the estate, and then repeated the effort on the reserve. I sampled both the northern and the southern parts of the estate. Sites in the northern part were a random subset of sites from the original 25 sampled by Fox and Hockey (2007) (n=12, site numbers: 1,3,5,6,7,8,13,16,17,20,22,24). I specifically included one body of water in the northern section of the estate to ensure that all habitat types were sampled. Given the north is approximately double the area of the south and to standardize for sampling effort, I included seven randomly selected sites in the south resulting in a total of 20 sites in the estate (Figure 5.1). I ensured a minimum distance of 200 m between sampling points so that point counts could be considered independent (Sutherland, 2006). I sampled around the estate, including patches in close proximity to residential gardens, which can provide important habitat for birds (Gonçalves *et al.*, 2021), allowing the possibility of sampling birds contained within.

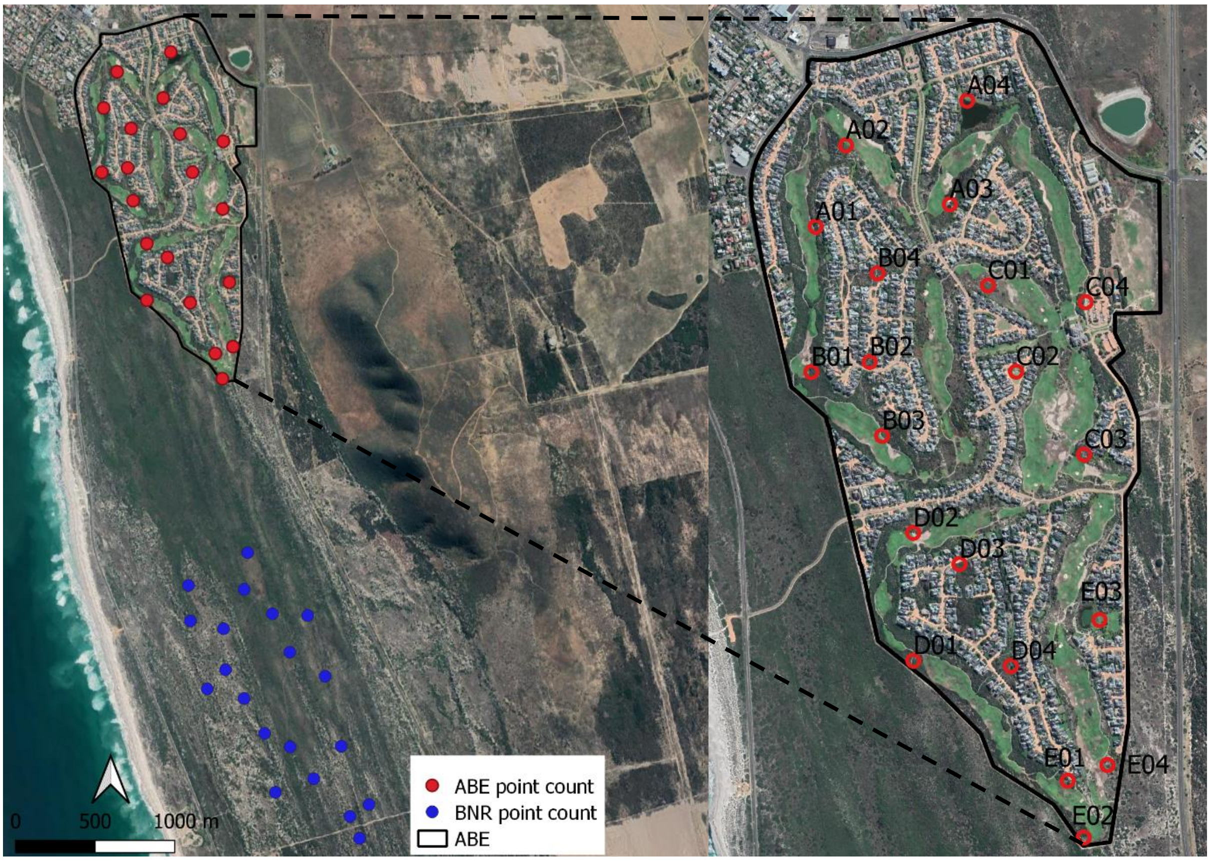


Figure 5.1: Point locations for bird counts within both the Atlantic Beach Estate (red points) and Blaauwberg Nature Reserve (blue points). Note the mirrored design between the estate (north) and reserve (south). The insert is an enlarged image of the estate, showing the station name and the layout of the estate with all locations in patches of natural habitat. Point counts were clustered into groups of four stations, which were all sampled in the same session. Point counts within the same cluster have the same letter.

To minimize confounding variables (e.g., time of day, weather) but avoid excessive travel time between locations I firstly grouped stations (n=4) that were close to one another into clusters (Figure 5.1; letters indicate respective clusters). I then randomly chose the order in which to visit each cluster and the stations therein. Clusters across both the estate and the reserve were included, so on a single day I could visit any combination of clusters on the estate and/or the reserve. Complete randomization of individual stations would have necessitated excessive travel. I visited each station a total of three times, ensuring I visited every station once before visiting any station twice and every station twice before I visited any station thrice. I could generally visit two clusters (eight stations) per day. I ensured that I visited each cluster at least once at the beginning of my morning, to correct for differences in bird presence between daybreak and mid-morning, when my sampling ended around 10:00 (Ralph, Droege and Sauer, 1995). I sampled for three weeks during spring (October and November of 2019) which corresponds to peak avian breeding season following winter rainfall and vegetation rejuvenation (Moreau, 1950). I performed all point counts between sunrise and 10:00, corresponding to the period when birds are most active and are therefore most likely to be visible for counting (Bibby, Burgess and Hill, 1992). I standardized sampling by avoiding days with strong wind, or extremes in rainfall or temperatures.

I followed a standard sampling procedure, which I repeated at each station. Upon arrival I began with a three-minute relaxation period to allow birds to become accustomed to my presence. Thereafter, I spent ten minutes recording all the birds I could identify, both visually and vocally. I used a pair of Nikon Action 8x42 binoculars for visual identification (Nikon Corporation, Minato City, Tokyo). I recorded the species, estimated distance from the observer, the activity the bird was engaged in at the time of first observation and the manner of detection (seen or heard). After the ten-minute sampling period, I randomly shuffled through calls of 16 “inconspicuous but responsive taxa” (Table 5.1). I played each call for 20 seconds using a JBL Flip 5 Waterproof Bluetooth Speaker (JBL consumer, Los Angeles, California), with the volume on the highest setting. I allowed 15 seconds of silence between each call. I recorded whether I had a response from a species and recorded any other new species which I had not observed during the initial ten-minute sampling period. I had hoped to use play backs from the same species as used by Fox and Hockey (2007), however despite repeated attempts, I was unable to obtain their species list. I therefore consulted Associate Professor Arjun Amar and Dr. Robert Thompson of the Percy Fitzpatrick Institute at the University of Cape Town, who suggested the 16 “inconspicuous but responsive taxa” likely to be used by the researchers (Table 5.1).

Table 5.1: The 16 "inconspicuous but responsive taxa" calls I used as playbacks as suggested by Associate Professor Arjun Amar and Dr. Robert Thompson from the Percy Fitzpatrick Institute at the University of Cape Town.

Common name	**Scientific name**
Bar-throated apalis	*Apalis thoracica*
Bokmakierie	*Telophorus zeylonus*
Cape bulbul	*Pycnonotus capensis*
Cape bunting	*Emberiza capensis*
Grey-backed cisticola	*Cisticola subruficapilla*
Levaillant's cisticola	*Cisticola tinniens*
Long-billed crombec	*Sylvietta rufescens*
Grey-winged francolin	*Scleroptila afra*
Cape grassbird	*Sphenoeacus afer*
Karoo prinia	*Prinia maculosa*
Cape robin-chat	*Cossypha caffra*
Karoo scrub robin	*Tychaedon coryphoeus*
Southern double-collared sunbird	*Cinnyris chalybeus*
Chestnut-vented warbler	*Sylvia subcoerulea*
Layard's warbler	*Sylvia layardi*
Pin-tailed whydah	*Vidua macroura*

Data analyses

I classified all flying birds as either "flying over" or "passing by." Birds that were "flying over" were engaging in a short range move within the site while birds that were "passing by" were flying at a considerable altitude and in a specific direction and were not considered to be using the site and were thus excluded from all analyses (Table 5.2).

Table 5.2: Bird species observed "passing by." These species were not included in any analyses. Unless otherwise stated, these species were seen from stations on both Atlantic Beach Estate and Blaauwberg Nature Reserve.

Common name	**Scientific name**
Greater flamingo[1]	*Phoenicopterus roseus*
Hartlaub's gull	*Larus hartlaubii*
Kelp gull	*Larus dominicanus*
Sacred ibis	*Threskiornis aethiopicus*
Spur-winged goose[2]	*Plectropterus gambensis*

[1]A flock of greater flamingo were observed only once passing by over Atlantic Beach Estate.
[2]Spur-wing goose were only observed passing by over Blaauwberg Nature Reserve.

Species richness is the total number of species present at a particular site. Evenness is how evenly the number of individuals are divided amongst the number of species (Table 5.3). Diversity incorporates both species richness and evenness, in essence calculating how well the number of individuals are split amongst the number of species, but also considering how many species are present. Evenness is scaled between 0 and 1, where 0 is the least even, while 1 is the most even. Diversity index interpretation depends on the index – the Simpson diversity index is interpreted in the same way as evenness, where it is scaled between 0 and 1, with values close to 1 representing high diversity (Magurran, 2004). Shannon-Wiener and Brillouin indices are similar in their interpretation, with higher values representing communities which are more diverse.

I incorporated both the Shannon-Wiener and Brillouin diversity indices. The Shannon-Wiener index has higher discriminatory power, but is more sensitive to unequal sampling (Magurran, 2004). The Brillouin index is often used, despite lower discriminatory power, as it accounts for unequal detection probabilities between different bird species (Magurran, 2004).

Table 5.3: Evenness and diversity indices, with associated formula for index calculation, and variables involved in calculating the index (Magurran, 2004).

Index	**Formula**	**Variables**
Pielou's evenness	$J' = \frac{H'}{Hmax}$	$Hmax$ = maximum possible diversity
Shannon-Wiener diversity index	$H' = -\sum p_i ln p_i$	p_i = proportion of individuals in the $_ith$ species
Brillouin index	$HB = \frac{lnN! - \sum ln n_i!}{N}$	n = total number of organisms of a particular species N = total number of organisms of all species
Simpson diversity index	$D = \sum {p_i}^2$	

I plotted the rarefaction curve using the *vegan* package (Oksanen *et al.*, 2019). Rarefaction curves allow one to compare the different stations in terms of species richness by standardising the sampling effort (Gotelli and Colwell, 2001). I used the station with the minimum number of observations and calculated a rarefied number of species at all other stations after an equivalent sampling effort.

I computed a correlation-based distance matrix for stations based on the Pearson's correlation measure in the R package *factoextra* (Kassambara and Mundt, 2020). Cluster analyses allow one to group similar sites according to various possible explanatory variables (in my case, species composition). The result is that sites within a cluster are more similar to one another than to sites in other clusters (within cluster variation is smaller than between cluster variation). I performed cluster analyses using the *factoextra* package in R (Kassambara and Mundt, 2020). I performed Non-metric Multi-dimensional Scaling (NMDS) in the *vegan* package in R (Oksanen *et al.*, 2019).

To test the similarity and dissimilarity between sites, I used the *anosim* and *simper* functions in the *vegan* package (Oksanen *et al.*, 2019). Initially I used the *vegdist* function in the *vegan* package to compute the Jaccard index. I performed an analysis of similarities (anosim) which tests whether there is a significant difference between two groups, in terms of species composition. I used 999 permutations and the Jaccard index to test for differences between the estate and the reserve. I then used the function *simper* (similarity percentages) to compute which species contributed most to the dissimilarity between sites.

Multiple linear regression model predictors (see Appendix 5.3 for values)

Distance to BNR

Urbanization alters bird communities (Chace and Walsh, 2006). These changes are not consistent across all species, with some species thriving in urban areas, while others disappear entirely (McKinney, 2002). I predicted that urban exploiting birds would have an increased prevalence nearer the middle of the estate (i.e., a larger distance from the reserve) which is the most urbanized section of the study area, while other species would only be found close to the edge of the estate (i.e., a smaller distance from the reserve). I chose distance to the nature reserve, as opposed to distance to edge, because the estate is bordered by Melkbosstrand to the north, and I wanted to observe the influence of distance to nearest natural habitat.

Distance to edge

The confluence of different habitats are physically and biologically different to the interior of each individual habitat (Saunders, Hobbs and Margules, 1991). These edge habitats are particularly pertinent where natural habitats meet the urban edge, creating a novel ecosystem, with new combinations and abundances of species previously unseen in a particular environment (Hobbs *et al.*, 2006). Edges thus present both challenges and opportunities to various species. Distance to edge incorporates distance to human settlement which makes up the reserve's southern boundary (discussed below) and by the presence of a major road, which acts as the reserve boundary on two sides and generally decreases bird abundance (Reijnen and Foppen, 2006). I predicted that bird species richness would decrease as one moves closer to the reserve edge.

Distance to settlement

I included distance to settlement as a predictor variable in reserve models, mainly because of the species associated with human settlements. These species have the potential to penetrate natural areas, potentially altering the species richness. I predicted an increased prevalence of bird species associated with humans, but a decrease in species richness generally.

Normalized Difference Vegetation Index (NDVI)

NDVI values have been found to increase with increasing plant cover (Martinuzzi *et al.*, 2008). NDVI can therefore be used as a proxy for vegetation cover and plant productivity and is calculated as:

$$\frac{NIR - red}{NIR + red}$$

where *NIR* is the near-infrared light, which plants largely absorb, and *red* light, which plants largely reflect, as measured by a satellite sensor (Pettorelli *et al.*, 2011). I used satellite imagery from the Sentinal 2 satellite at 10 meter resolution taken during the sampling and later extracted through the *sen2r* package in R (Ranghetti and Busetto, 2020; Ranghetti *et al.*, 2020). Bird species richness has been found to be strongly correlated with NDVI, in both rural and urban environments (Bino *et al.*, 2008; Shirley *et al.*, 2013). I thus predicted that species richness would correlate positively with higher NDVI.

Water

The presence of water increases bird species richness in urban areas (McKinney, Raposa and Cournoyer, 2011). I sampled at the only two permanent, perennial sources of water on the estate. Human habitation can introduce sources of water, such as bird baths, which I could not wholly quantify. I therefore included water as a binary variable with two levels (i.e., at a water body or not at a water body) for each sampling site as opposed to a continuous variable (distance to water). I predict a higher species richness at bodies of water. There is no permanent water in the nature reserve and hence I did not include this variable as a predictor in reserve linear models.

Multiple linear regression model specifics

I checked for collinearity between variables by using variance inflation factors (VIF) in the R package *car* (John *et al.*, 2020), with species richness as the response variable. None of the variables I used together were deemed to be collinear, defined as having VIF scores greater than five (Dormann *et al.*, 2013). I plotted each of my variables against species richness to observe whether they had a linear effect. One variable (distance to natural land) appeared to have a quadratic effect, and hence I included it as such in my model.

I fitted multiple linear regression models, using different combinations of the abovementioned predictors. I computed summary statistics for each model, and compared model fit on the basis of corrected Akaike's Information Criterion (AICc) using the *AICcmodavg* function in R (Mazerolle, 2020). Models with the lowest ΔAICc values were considered the best fit to these data (Hurvich and Tsai, 1989). I checked the assumptions of these models by plotting residuals against fitted values. I then visualized the output of the best fitting model using the *visreg* function in R (Breheny and Burchett, 2020).

Functional diversity

Calculating functional diversity requires four distinct steps: constructing a trait matrix, converting the trait matrix into a distance matrix, plotting the distances as a dendrogram and calculating the branch lengths of the dendrogram (Petchey and Gaston, 2002). In my trait matrix I included traits for breeding strategy, feeding strategy, food type, nest construction or use and resource quantity, all of which I extracted from Hockey, Dean and Ryan (2005) (Table 5.4). These traits relate to the resource quantity required by species and how they acquire these resources (Seymour *et al.*, 2015). I standardized continuous traits (i.e., average clutch size and weight) to have a mean of zero and a standard deviation of one (Petchey and Gaston, 2006). Within the matrix, for all species, across all binary traits, I allocated a "1" to indicate presence of a particular trait in a particular species, and "0" to indicate absence. To ensure equal weighting of all traits in a specific trait type, I divided each trait by the number of traits within that trait type. For example, there were nine traits within the "feeding strategy" trait type and so I divided each trait by nine. Thus an alpine swift (*Tachymarptis melba*) being exclusively an aerial feeder received a score of 1/9 in the feeding strategy trait type (Laliberté and Legendre, 2010). I created a Gower dissimilarity matrix using the *vegdist* function in the R package *vegan* (Gower, 1971; Oksanen *et al.*, 2019). I made a distance matrix using *upgma* function, plotted the dendrogram and calculated the branch length for each species in the R package *phangorn* (Schliep *et al.*, 2019). To calculate the functional diversity at each station, I calculate the mean functional diversity of all the species occurring at a station. I calculated the average functional diversity per station at both sites and performed a one-sample t-test to compare whether the estate had a higher average functional diversity than the reserve.

Table 5.4: Trait type, specific trait and trait scale used to determine differences in functional diversity between Atlantic Beach Estate and Blauwberg Nature Reserve. These data were extracted from work by Hockey, Dean and Ryan (2005).

Trait type	**Trait**	**Scale**
Breeding	Brood parasite	Binary
Feeding strategy	Aerial	Binary
	Aquatic	Binary
	Canopy gleaner	Binary
	Digs in ground	Binary
	Ground surface feeding	Binary
	Hovers	Binary
	Perch and swoop	Binary
	Shrub	Binary
Food	Bulbs, corms, rhizomes, roots	Binary
	Carrion	Binary
	Marine fish, invertebrates	Binary
	Nectar, pollen	Binary
	Foliage, herbs	Binary
	Freshwater fish, invertebrates	Binary
	Fruit	Binary
	Intertidal invertebrates	Binary
	Seeds	Binary
	Terrestrial invertebrates	Binary
	Terrestrial vertebrates	Binary
Nest	Burrow	Binary
	Cavity maker	Binary
	Cavity user	Binary
	Constructed mud	Binary
	Floating	Binary
	Ground	Binary
	Hanging	Binary
	Over water	Binary
	Supported	Binary
Resource quantity required	Average clutch size	Continuous
	Weight	Continuous

I classified species into functional groups following the methods outlined by Cumming and Child (2009) and (Şekercioğlu, 2006) using data from Hockey, Dean and Ryan (2005). These guilds consider the ecological functions and ecosystem services provided by birds (Şekercioğlu, 2006). I considered nine different functional groups: ecosystem engineers, granivores, grazers, insectivores, nutrient movers, pollinators, raptors, scavengers and seed dispersers. I allocated a "1" if a particular species was classified as being part of a particular functional group and a "0" if a species was not. Importantly, species can belong to more than one functional group. Additionally, note that although I use familiar nomenclature (e.g., raptor), this is not necessarily consistent with the use of that specific term elsewhere. Thus I consider egrets and herons to be raptors because they hunt small vertebrates. I summed the total number of species in each functional group, which I did independently for the estate and the reserve. I then used a Pearson's Chi-squared test for independence to compare proportions of each functional group on the estate and the reserve with proportions for 950 species across southern Africa, as computed by Cumming and Child (2009).

Results

I observed 83 bird species across the 120 individual point counts I conducted across all 40 stations (20 stations on the estate and 20 on the reserve) with 77 species on the estate and 57 on the reserve. There were 51 bird species common to both sites (Appendix 5.1), while 26 bird species were found exclusively on the estate and 6 bird species were found exclusively in the nature reserve (Table 5.5).

Table 5.5: Common and scientific names for bird species found exclusively on Atlantic Beach Estate (ABE) or Blaauwberg Nature Reserve (BNR).

ABE		BNR	
Common name	**Scientific name**	**Common name**	**Scientific name**
African darter[1]	*Anhinga rufa*	African hoopoe	*Upupa africana*
Barn swallow	*Hirundo rustica*	Black-headed heron	*Ardea melanocephala*
Black-crowned night heron[1]	*Nycticorax nycticorax*	Black-winged kite	*Elanus caeruleus*
Blacksmith lapwing[1]	*Vanellus armatus*	European bee-eater	*Merops apiaster*
Cape sugarbird[2]	*Promerops cafer*	Grey-winged francolin[2]	*Scleroptila afra*
Common buzzard	*Buteo buteo*	Little bittern[1]	*Ixobrychus minutus*
Common moorhen[1]	*Gallinula chloropus*		
Common waxbill	*Estrilda astrild*		
Dusky sunbird[2]	*Cinnryis fuscus*		
Greater striped swallow	*Cecropis cucullata*		
Grey heron[1]	*Ardea cinerea*		
Hadeda ibis	*Bostrychia hagedash*		
House sparrow	*Passer domesticus*		
Jackal buzzard[2]	*Buteo rufofuscus*		
Little egret[1]	*Egretta garzetta*		
Malachite sunbird	*Nectarinia famosa*		
Olive thrush	*Turdis olivaceus*		
Pin-tailed whydah	*Vidua macroura*		
Purple heron[1]	*Ardea purpurea*		
Red-knobbed coot[1]	*Fulica cristata*		
Red-winged starling	*Onychognathus morio*		
Southern masked weaver	*Ploceus velatus*		
Spotted thick-knee	*Burhinus capensis*		
Water thick-knee[1]	*Burhinus vermiculatus*		
White-throated swallow	*Hirundo albigularis*		
Yellow-billed kite	*Milvus aegyptius*		

[1] Birds closely linked to water.
[2] Species endemic to southern Africa.

In addition to having a higher absolute species richness, the estate was more even and more diverse than the reserve across a range of different metrics (Table 5.6).

Table 5.6: Species richness, Pielou's evenness, Shannon-Wiener diversity index, Brillouin index and Simpson diversity index values for Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR).

	Species richness	**Pielou's evenness**	**Shannon-Wiener diversity**	**Brillouin index**	**Simpson diversity**
ABE	79	0.78	3.38	3.33	0.95
BNR	57	0.75	3.05	2.99	0.92

Sites on the estate generally had more rapid rates of species accumulation than sites on the reserve (Figure 5.2). Station 37 (on the reserve) had the lowest number of observations (n=70), yielding 20 species. At the same sampling effort (i.e., after 70 observations) site 28 on the reserve had the lowest rarified species richness (S=18.13), while site 36 on the reserve had the highest rarified species richness (S=26.55). Site 19 on the estate had the highest overall species richness and the highest total number of birds (S=41, n =300).

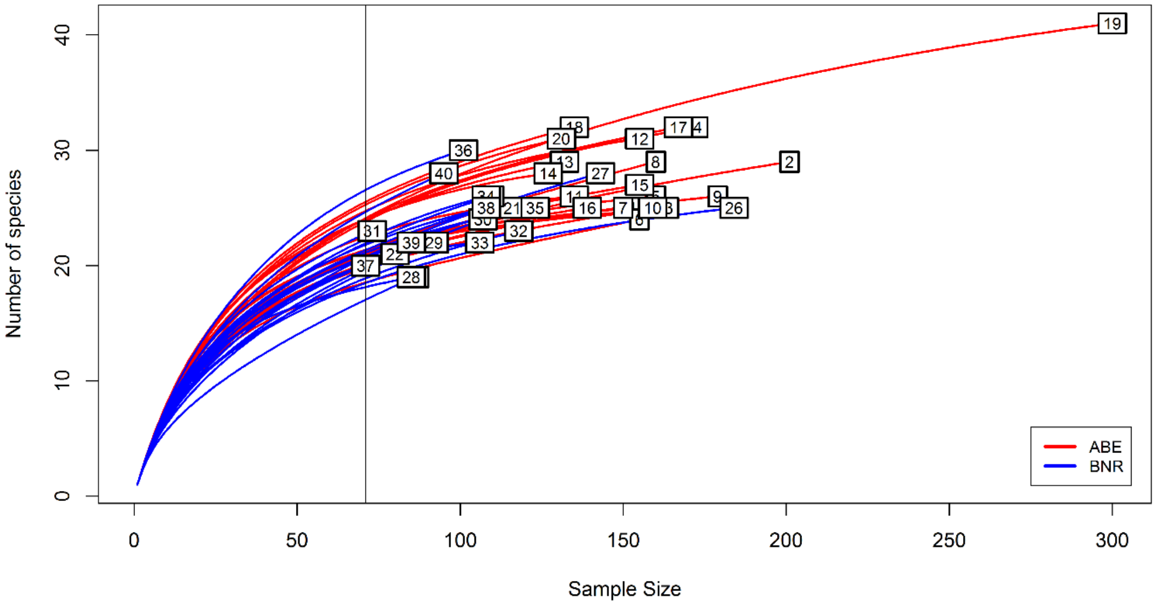


Figure 5.2: Sample-based rarefaction for each station in Atlantic Beach Estate (red lines) and Blaauwberg Nature Reserve (blue lines). The horizontal line at n=70 indicates the station with the lowest sample size (station 37), against which all other stations are standardized.

Cluster analysis revealed three distinct station clusters (Figure 5.3). Cluster one comprised stations 4 and 19, which were on the estate, cluster two comprised all stations in the reserve plus station 18 from the estate, while cluster three comprised the remaining stations on the estate. Cluster two and three were relatively similar, while cluster three was less similar (Figure 5.3).

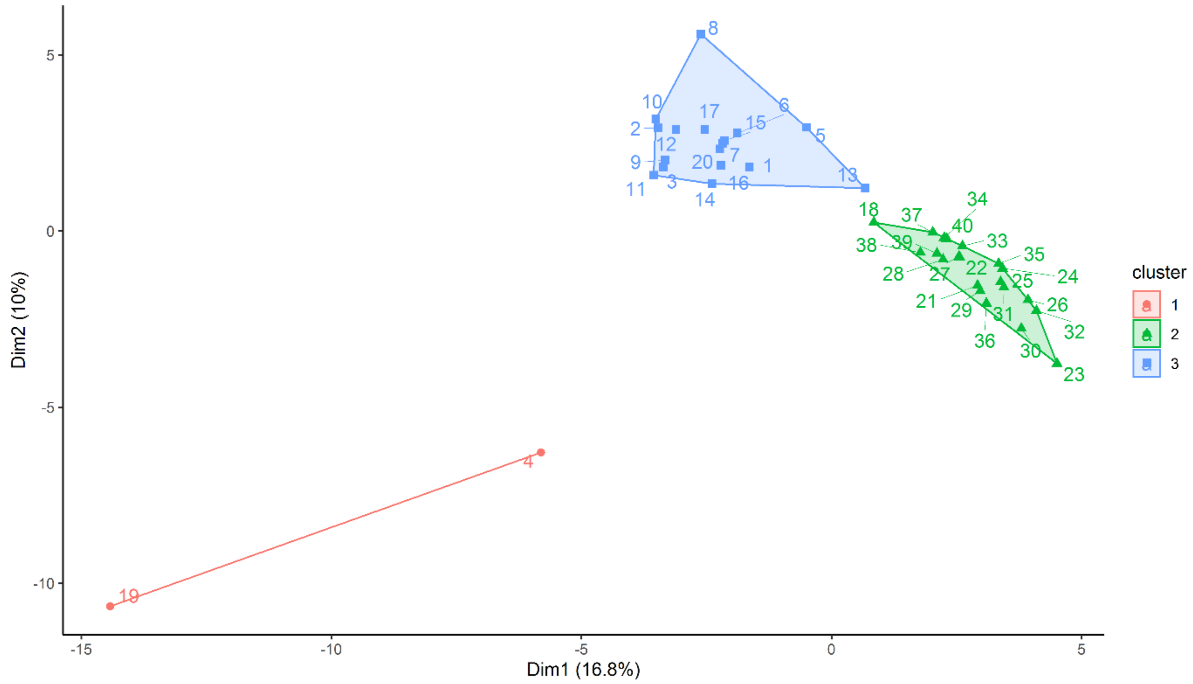


Figure 5.3: Cluster analysis (n=3 clusters) of bird species from 40 sampling stations across Atlantic Beach Estate and Blaauwberg Nature Reserve. Numbers 1 to 20 are stations found on the estate, while numbers 21 to 40 are stations located on the reserve.

Differences between sites, and similarities across stations within sites was confirmed by Non-metric Multi-dimensional Scaling (NMDS). Once again, sites generally clustered together according to site. Exceptions are stations 4 and 19, which clustered together, away from other estate stations and station 18 which lay between the main estate stations and reserve stations (Figure 5.4).

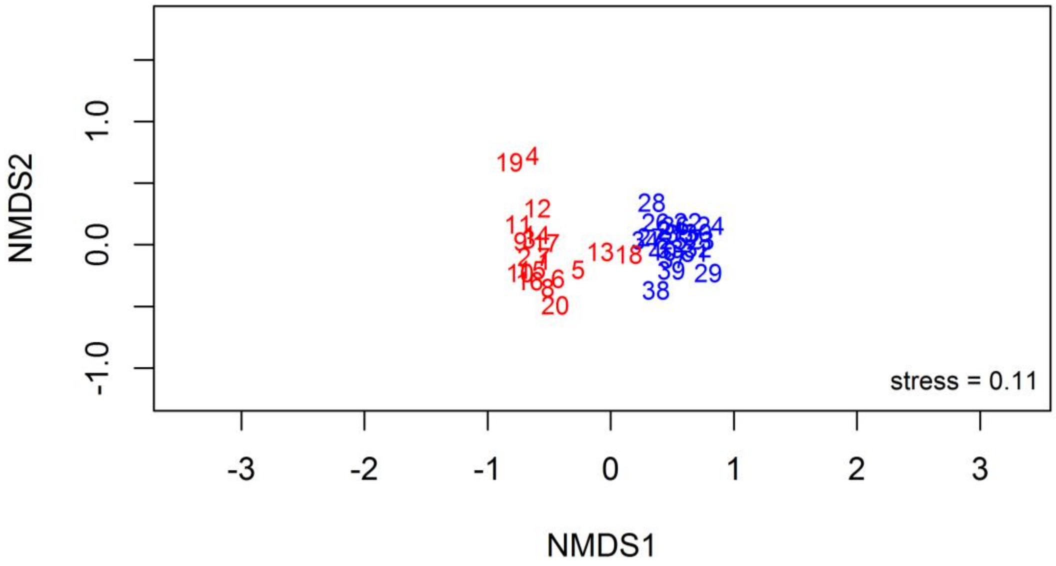


Figure 5.4: Non-metric Multi-dimensional Scaling (NMDS) of bird species composition from 40 sampling stations across Atlantic Beach Estate and Blaauwberg Nature Reserve. Numbers 1 to 20 (shown in red) are the 20 stations on the estate, while numbers 21 to 40 (shown in blue) are the 20 stations on reserve. Stress is a measure of fit, with values of approximately 0.1 deemed to have fair fit.

The estate and the reserve had significantly different species compositions (R=0.9, p=0.001). Common starling contributed the most to the dissimilarity between species composition on the estate and the reserve, having a high prevalence on the estate but a low prevalence on the reserve (Table 5.7). In contrast Karoo scrub robin (*Cerotrichas coryphoeus*) had a low prevalence on the estate but a high prevalence on the reserve and as a result were the second most important contributor to the dissimilarity between sites (Table 5.7). Many other species were observed multiple times on one site, while infrequently on the other, making a large contribution to the dissimilarity between sites (Table 5.7).

Table 5.7: The 10 species which contributed most to the dissimilarity between sites. The table includes the average percentage contribution, standard deviation (SD), mean species abundance on Atlantic Beach Estate (ABE), mean species abundance on Blaauwberg Nature Reserve (BNR) and associated permutation p-value.

Species	**Average % contribution**	**SD**	**Mean ABE abundance**	**Mean BNR abundance**	**p-value**
Common starling	7	3.36	19.10	0.80	0.001
Karoo scrub robin	6.6	2.79	1.30	18.85	0.001
Cape sparrow	6.5	3.85	20.45	6.30	0.001
Karoo prinia	2.9	1.78	7.70	14.25	0.002
Cape bulbul	2.9	2.10	5.70	11.75	0.006
Southern red bishop	2.6	4.77	8.10	0.45	0.001
White-rumped swift	2.5	1.89	6.85	0.25	0.001
Speckled pigeon	2.4	1.32	6.60	0.65	0.001
Cape wagtail	2.3	2.17	6.05	0.05	0.001
Laughing dove	2.2	2.76	6.10	0.15	0.001

Common starling, Karoo scrub robin and Cape sparrow (*Passer melanurus*), contributed most to the dissimilarity between sites, and were linked to strong disparities in prevalence between sites (Figure 5.5). Common starling were seen ubiquitously across the estate with some 382 observations in the estate, but only 16 observations in the reserve. While the estate included most species found on the reserve, some fynbos species (e.g., Karoo scrub robin) were found either at a lower density or seen only in patches at the edge of the estate and bordering the reserve (Figure 5.5). The Karoo scrub robin was seen ubiquitously across all stations in the reserve ranging between 8 and 32 observations, while on the estate the range was between 0 (for all but 4 sites) and 6 independent observations, all of which were at sites bordering the perimeter fence. Cape sparrow observations mirror those of common starling with observations across all stations totaling 409 observations on the estate, and only 126 observations on the reserve, primarily at sampling stations along the south-western boundary (Figure 5.5).

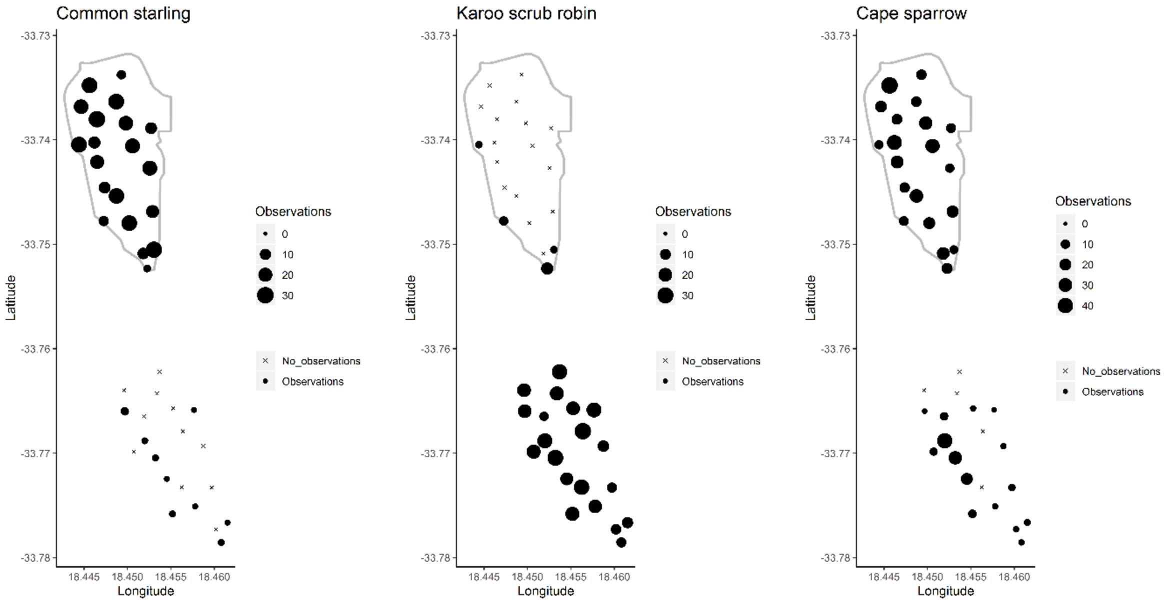


Figure 5.5: Abundance and distribution of common starling (left), Karoo scrub robin (centre) and Cape sparrow (right) across Atlantic Beach Estate (top outline) and Blaauwberg Nature Reserve (lower clump). Larger circles indicate a higher number of observations. Stations with no observed individuals are marked by an “x”, to indicate the position of each station. Note the number of observations varies between species.

I ran four different linear regression models to predict species richness across stations on the estate (Table 5.8). I ran each of my explanatory variables individually first, and then combined variables and included distance to natural land as having a quadratic effect.

Table 5.8: Linear regression models predicting species richness at sites in Atlantic Beach Estate ranked according to corrected Akaike Information Criterion (AICc) scores and other selection criteria (p-value, F-statistic and standard error). Species richness was the response variable, while water, distance to Blaauwberg Nature Reserve (Reserve) and NDVI were predictor variables (see Appendix 5.3 for values).

Model formula	AICc	ΔAICc	p-value	F-statistic	SE
$S_1 = \beta_0 + \beta_1 \text{Water} + \beta_2 (\text{Reserve})^2$	104.982	0	<0.001	9.756	2.612
$S_2 = \beta_0 + \beta_1 \text{Water}$	106.218	1.236	<0.001	16.1	3.009
$S_3 = \beta_0 + \beta_1 \text{Reserve}$	115.639	10.658	0.086	3.29	3.808
$S_4 = \beta_0 + \beta_1 \text{NDVI}$	118.952	13.97	0.842	0.041	4.137

The best fitting model (S_1) included water as a categorical variable and distance to natural land as a quadratic explanatory variable. The second best fitting model (S_2), had only water as an explanatory variable, with a small difference in AICc (Δ=1.236), indicating similar support for both models (Burnham and Anderson, 2002). However, S_1 was a better fit for these data, explaining 58 % of the variance (F=9.756 (3/16 df), p<0.001), while S_2 explained 44.3 % of the variance (F=16.1 (1/18 df), p<0.001). The presence of water was a significant predictor of station species richness on the estate, while distance to reserve improved model fit (β_{Water} =9.36, p<0.001; $\beta_{Reserve}$ =-5.45, p=0.054; $\beta_{(Reserve)^2}$ =4.93, p=0.084). The presence of water at the sampling station increased the station species richness, while distance to edge has a parabolic effect, with higher species richness predicted both close and far from natural areas but low species richness at intermediate distances away from natural land (Figure 5.6).

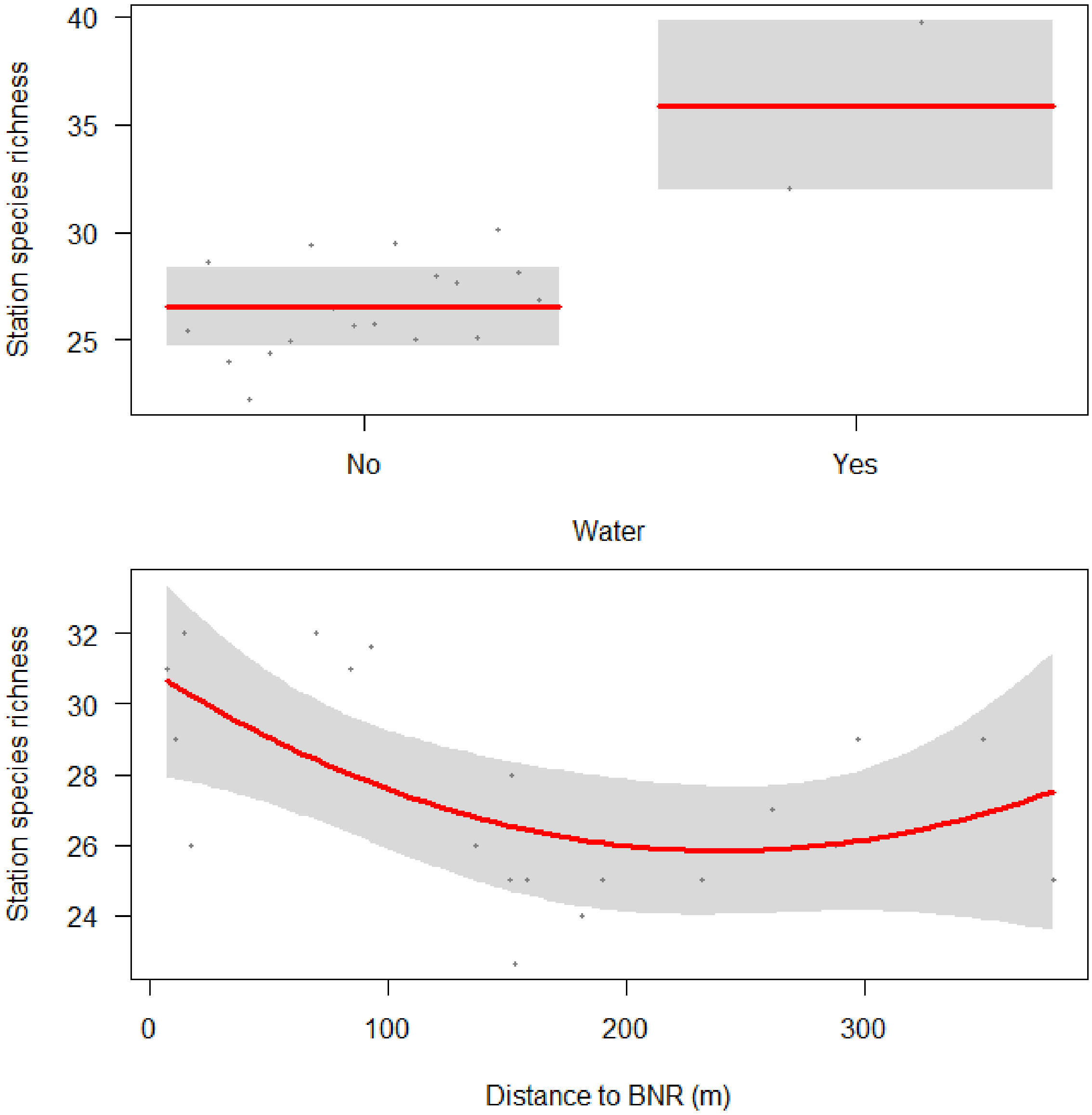


Figure 5.6: Multiple regression model showing influence of water and distance to BNR on predicting species richness at stations on Atlantic Beach Estate (Adjusted R^2=0.58, p-value<0.001). Grey lines indicate 95 % confidence intervals.

On the reserve I used distance to edge, distance to settlements and NDVI as predictors of species richness, however none of these models had significant predictive power, with the best-fitting model explaining only 1.9 % of the variance (Table 5.9). I did not consider this to have suitable fit, and hence have not considered these models any further.

Table 5.9: Linear regression models predicting species richness at sites on Blaauwberg Nature Reserve ranked according to corrected Akaike Information Criterion (AICc) scores and other selection criteria (p-value, F-statistic and standard error). Species richness was the response variable, while distance to settlement, distance to edge and NDVI were predictor variables (see Appendix 5.3 for values).

Model formula	AICc	ΔAICc	P-value	F-stat	SE
$S = \beta_0 + \beta_1$Disttosettlement	105.580	0	0.259	1.359	2.962
$S = \beta_0 + \beta_1$Disttoedge	105.849	0.269	0.308	1.1	2.982
$S = \beta_0 + \beta_1$NDVI	107.024	1.174	-0.055	0.01	3.07

Stations on the estate had a significantly higher mean functional diversity for bird species than stations on the reserve (t=1.9098, df=36.231, p-value=0.032) (Figure 5.7).

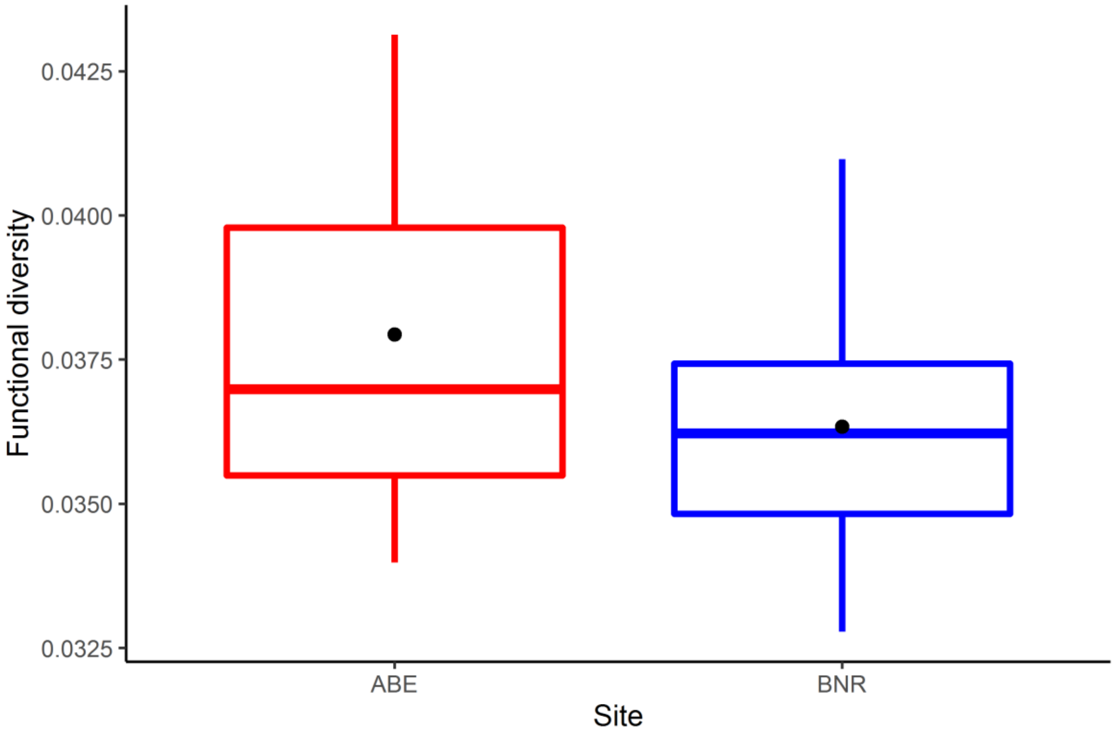


Figure 5.7: Mean functional diversity of species at each station on Atlantic Beach Estate (red) and Blaauwberg Nature Reserve (blue).

In addition to having a higher mean functional diversity, the estate had similar percentages of functional groups when compared to the reserve, and both had a similar composition when compared to the rest of southern Africa (χ^2 = 34.376, df = 16, p-value = 0.005) (Figure 5.8).

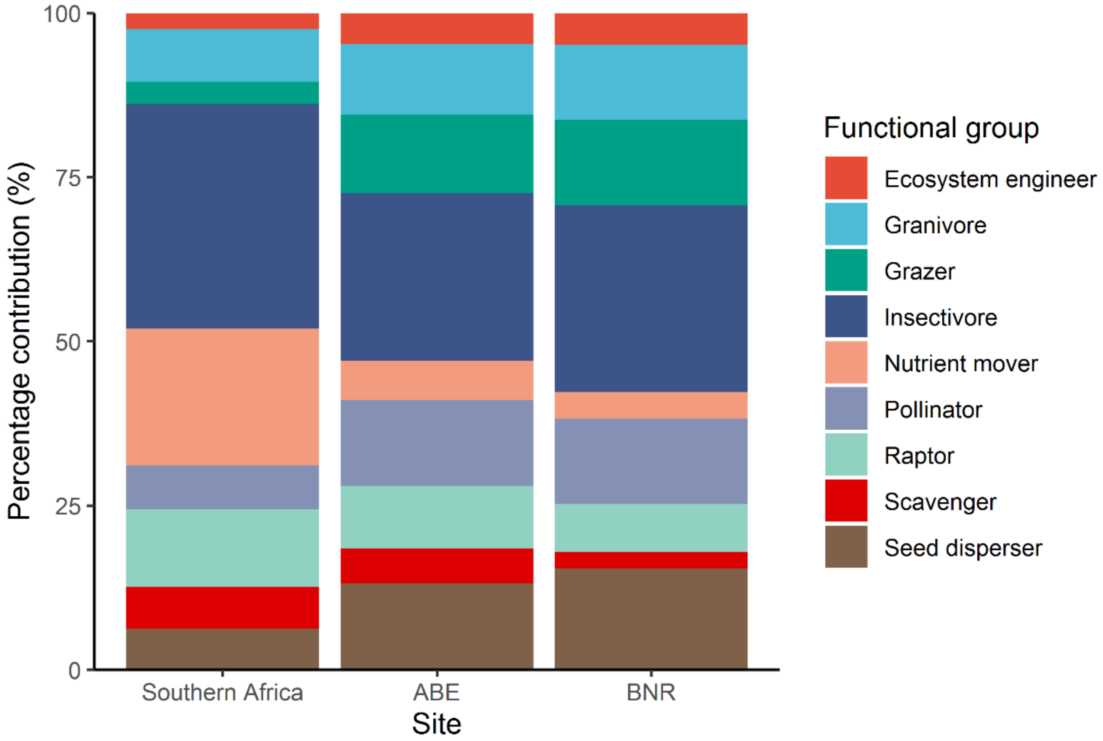


Figure 5.8: Southern Africa, Atlantic Beach Estate (ABE) and Blaauwberg Nature Reserve (BNR) have a similar proportion of species from the nine different functional groups.

Discussion

Why do the estate and the reserve share so many species?

Almost 90 % of the bird species I observed on the reserve were also observed on the estate (n=51/57). The estate borders the reserve to the south, west and east. As a result, highly mobile species such as birds can move freely between the two sites. This is particularly likely given the small size of the estate with the innermost sample site on the estate being only 379 m from the perimeter fence. Peri-urban landscapes which retain natural vegetation are often able to harbor more species than those that don't (Chace and Walsh, 2006; Threlfall *et al.*, 2017; Villaseñor, Escobar and Hernández, 2021). The short distances between patches of natural habitat within the estate means that no species are likely to be isolated to specific patches (Desrochers and Hannon, 1997; Melles, Glenn and Martin, 2003; Silva *et al.*, 2020) and are thus able to exploit resources from the entire mosaic of natural and transformed habitats (Dunning, Danielson and Pulliam, 1992). I cannot infer from these data whether there is a source-sink relationship between the two sites (Pulliam, 1988; Runge, Runge and Nichols, 2006). However, if the estate were found within an entirely urban landscape without possible supplementation from a natural reserve, one would assume the species composition would be quite different and species richness and diversity would be lower.

Differences between the estate and the reserve

While there is a large degree of overlap in species present at both sites (n=51), there are many species restricted to one of the two sites (n=26 on the estate and n=6 on the reserve) and thus the estate and the reserve do harbor distinct bird communities. Previous studies exploring bird community changes across a shared landscape have found an increase in total biomass, but a decrease in diversity as one moves from a rural to an urban landscape (Cam *et al.*, 2000; Chace and Walsh, 2006; Batáry *et al.*, 2018). Urban areas are often associated with increased food availability, prevalence of roosting sites and protection from natural predators leading to an increased abundance of birds, but a decrease in species richness, with these communities being dominated by a few urban exploiting, often introduced species (Cam *et al.*, 2000; McKinney, 2002). The peri-urban landscape however lies somewhere in the middle, reaping the benefits of the presence of natural and urban land and is therefore classified as an area of intermediate disturbance

Bird diversity peaks in places of intermediate disturbance (Roxburgh, Shea and Bastow Wison, 2004; Malavasi, Battisti and Carpaneto, 2009; Pal *et al.*, 2019), as most native species persist, and species richness is bolstered by invading urban exploiters (Marzluff, 2001, 2005). The estate seems to fit the profile of an intermediately disturbed habitat – it contains numerous patches of natural land interspersed with landscaped gardens, a golf course, artificial water bodies and surrounded by a nature reserve. Golf courses may support a greater number of avian species than surrounding nature reserves, however they do not necessarily maintain the species composition found in nature reserves, as native bird species may be replaced by widely distributed generalists (Blair, 1996; Nooten *et al.*, 2018). The mosaic of natural and human modified landscapes with a low density of people may explain why the estate hosts a large community of generalist species, while still retaining a substantial variety of native species.

Outlier stations

Stations 4 and 19 cumulatively accounted for six species not found at any other station, partly as a result of being located at sites of permanent water which included the presence of a number of obligate water users (black-crowned night heron (*Nycticorax nycticorax*), common moorhen (*Gallinula chloropus*), purple heron (*Ardea purpurea*), red-knobbed coot (*Fulica cristata*) and water thick-knee (*Burhinus vermiculatus*)) (Hockey, Dean and Ryan, 2005). Permanent water is known to increase bird species richness in urban areas, because of an increased availability of food and vegetation in which to shelter or nest, and the presence of a different habitat (Hodgkison, Hero and Warnken, 2007;

McKinney, Raposa and Cournoyer, 2011; Nooten *et al.*, 2018). I sampled at the only two sites of permanent water on the estate, and there is no permanent water in the coastal sector of the reserve and hence few obligate water users persist at this site. Unexpectedly station 19 was the only site I observed Cape sugarbird (*Promerops cafer*), and only once, though this species has been observed in gardens close to nature reserves (Hockey, Dean and Ryan, 2005; Coetzee, Barnard and Pauw, 2018).

Stations 13 and 18 were also considered to be outliers and were situated in the southern portion of the estate, bordering the nature reserve and buffered from residential areas by the golf course. These two stations are thus located further from human settlement than any other stations within the estate and are located within large patches of remnant Strandveld near the natural habitat of the reserve. In essence therefore these two locations are arguably more similar to the reserve than they are to most other locations within the estate revealing the importance and usefulness of birds as bioindicators of habitat transformation (Bibby, 1999; Mistry, Berardi and Simpson, 2008; Herrando *et al.*, 2014).

What species are found on the estate but not the reserve?

Some bird species thrive in human modified landscapes (McKinney, 2002; Guetté *et al.*, 2017). Humans bring with them a number of potential benefits to bird species, which might increase their prevalence, including permanent water bodies, roosting sites, additional food supplies and non-native vegetation (Hockey, 2003; Fuller *et al.*, 2008). As a result, a number of urban exploiting species have seen range expansions across southern Africa effectively following the growing human footprint (Hockey, 2003; Harebottle, 2016). In addition to water birds this included blacksmith lapwing (*Vanellus armatus*), hadeda ibis, house sparrow and red-winged starling (*Onychognathus morio*).

Nectarivorous birds play a crucial pollination role in the highly species rich Cape Floristic Region. The region has 318 bird pollinated plants (Rebelo, 1987), but only four resident pollinators fulfill this role (Cape sugarbird, malachite sunbird (*Nectarinia famosa*), southern double-collared sunbird (*Cinnyris chalybeus*) and the orange-breasted sunbird) (Rebelo, Siegfried and Crowe, 1984). Each of these species is relatively specialized in terms of the floral species it pollinates, hence they are functionally different, and the loss of one species cannot be substituted by the addition of another (Geerts and Pauw, 2009; Geerts, 2016). With the exception of southern double-collared sunbirds, nectarivores in the cape floristic region do not persist well in urban landscapes (Pauw and Louw, 2012). Malachite sunbirds venture a maximum of one km into urban landscapes, while Cape sugarbirds display visible signs of stress when in close proximity to humans (Pauw and Louw, 2012; Mackay *et al.*, 2017). That these species were found on the estate is a good indicator of decent vegetation quality and minimal human disturbance.

The estate potentially provides many unique opportunities to nectarivorous species not found on the reserve. The highly heterogeneous estate may better cater to the different floral preferences of the different species, while the nature reserve is more homogenous in vegetation (Rebelo, Siegfried and Crowe, 1984; Geerts and Pauw, 2009). Additionally this diversity in plant species on the estate might result in there being a longer floral season, as different species of plant come into bloom at different times of the year (Coetzee, 2016). Generally, fynbos dwelling nectarivores migrate locally, following blossoming flowers (Coetzee, 2016). The presence of a wide array of species which flower at different times throughout the year may facilitate the presence of these species on the estate, while being absent in the nature reserve. Estate residents may also directly contribute to increased prevalence of these species by placing bird baths and artificial nectar sources in their gardens (Coetzee, Barnard and Pauw, 2018, 2021).

Which species contributed most to the dissimilarity between the estate and the reserve?

Three species contributed to over 20 % of the dissimilarity between sites by having a much higher prevalence at one site. These were the common starling, Karoo scrub robin and the Cape sparrow. The common starling is an invasive species, which has steadily expanded its range since it was first introduced to Cape Town in 1899 (Ivanova and Symes, 2018; Shivambu, Shivambu and Downs, 2020). Both the common starling and the Cape sparrow are closely linked to humans (Hockey, Dean and Ryan, 2005; Fuller, Tratalos and Gaston, 2009; Kopij, 2013). By contrast, I observed Karoo scrub robin ubiquitously across the reserve, but only at sites on the southern border of the estate, which are furthest away from humans and closest to the nature reserve, suggesting that this species has a low tolerance to human modified land (Fox and Hockey, 2007). Of the ten species which contributed most to the difference between sites, four are endemic to southern Africa (Cape bulbul (*Pycnonotus capensis*), Cape sparrow, Karoo scrub robin and Karoo prinia (*Prinia maculosa*)) (Hockey, Dean and Ryan, 2005). While Cape sparrow were far more abundant on the estate, the other three species were more abundant in the reserve. Though the estate may support populations of these three endemic species, these findings raise concern that locally occurring endemic species are being replaced by widely occurring generalists in urban transformed habitats.

Comparisons with Fox and Hockey (2007)

A previous bird survey conducted on the estate and the reserve found that bird diversity and abundance was higher in the reserve than on the estate (Fox and Hockey, 2007). In particular the authors observed an increased prevalence of granivores, generalists and species favouring ecotonal habitats (i.e., transitional habitats) on the estate, but a decreased prevalence of nectarivores and frugivores when compared to the reserve (Fox and Hockey, 2007). The authors highlighted the critical role of nectarivores and frugivores in the Strandveld habitat because of the key role species in these guilds play in pollination and seed dispersal (Rebelo, 1987; Knight, 1988; Fox and Hockey, 2007). The authors concluded by suggesting that bird abundance and diversity on the estate was likely to decrease further because of relaxation effects (the process whereby communities settle and equilibrium and immigration matches emigration) (Diamond, 1972) and because the small patches found on the estate are highly susceptible to edge effects, such as the invasion of Kikuyu grass.

I also observed an increased prevalence of granivores, generalists and species favouring ecotonal habitats on the estate. This manifested itself in there being several species from these guilds present on the estate, but not present in the reserve. However, instead of the previously observed decline in nectarivores, I observed a higher species richness of birds in this guild on the estate compared to the reserve. I observed only the Southern double-collared sunbird on the reserve, while on the estate, I observed the Southern double-collared sunbird and an additional three nectarivores (namely Cape sugarbird, dusky sunbird and malachite sunbird). This could be because of the fact that the nectar producing fynbos flowers which these nectarivores require for survival take a number of years to reach maturity and produce flowers (Midgley and Rebelo, 2008). Given that the previous study was conducted shortly after the construction of the estate, private gardens (which often contain nectar producing flowers) and the estate generally had not yet been established, or their plants were not yet old enough to produce flowers. In general, my study refutes the key predictions of Fox and Hockey (2007) with higher abundance and diversity of bird species on the estate.

Functional diversity

Suburban water has been found to increase functional diversity of birds in Cape Town (Suri *et al.*, 2017). It therefore comes as no surprise that the estate has a higher average functional diversity than the reserve, even when accounting for differences in the number of species observed at each site. What I find more interesting is that both sites have similar proportions of the different functional groups, and that these proportions are similar to those for southern Africa as a sub-region. However, the transformation of natural land has been observed to bring about a decreased prevalence of insectivores, pollinators, raptors and scavengers in South Africa (Child, Cumming and Amano, 2009). While the estate did not have significantly different proportions of functional groups, all species found on the reserve but not on the estate were either raptors and/or insectivores (grey-winged francolin are considered both grazers and insectivores). Despite the loss of various raptors and insectivores from the estate, these species were however replaced by other raptors and insectivores not found on the reserve.

Conclusion and recommendations

In general, the estate appears to be a better site for bird species than the reserve. The estate harbored a more diverse array of species than the reserve, driven primarily by the presence of permanent water on the estate, including many species which contribute greatly to the environment and are sensitive to human disturbance (e.g., sunbirds and the Cape sugarbird), resulting in a higher alpha diversity (i.e. local scale diversity) (Whittaker, 1972). These species may well have preferentially selected for the estate given the estate provided resources not found on the nature reserve. Many of the species found on the estate, but not on the reserve are urban exploiters. These species benefit directly from human presence and thrive in urban areas throughout the country (e.g., hadeda ibis and red-winged starling (Hockey, 2003; Duckworth, Altwegg and Guo, 2010)). Other species may be found on the estate only because of the supplementary resources provided by the estate and hence the estate could not replace the role of the reserve. Thus, I suspect that some species preferentially select for the estate, while others happen upon the estate because of additional resources. In this study it seems as if both can persist and this may be a consequence of the proximity of a nature reserve to a low-density eco-estate allowing endemic species to persist, albeit at far lower densities on the estate than on the nature reserve.

Previous research on Strandveld birds concluded that maintaining structural and floristic diversity in a highly heterogeneous vegetation landscape is crucial to population persistence (Nalwanga *et al.*, 2004). The patches of natural land on the estate represent important pockets of this natural habitat in which many native Strandveld species persist. These patches must therefore be maintained, along with the linkages between patches, to facilitate the continued presence of many native species on the estate. However, while the estate is heterogeneous at a fine scale, at a broader scale it is more homogeneous than the reserve, adversely affecting the beta diversity (i.e., difference in diversity between local scale patches) (Whittaker, 1972). Within the fynbos biome both alpha and beta diversity are critically important (Cowling, 1990) and thus if eco-estates are scaled to a landscape level (through expansion) and large tracts of natural habitat become smaller and more isolated then overall avian diversity is predicted to decrease.

I was unable to quantify whether there are fitness costs for birds living on the estate. These might include a higher risk of mortality and exposure to pathogens and poisons, lower reproductive output, or increased stress which could impact the health and physical condition of individuals (Fretwell and Lucas, 1969; Mackay *et al.*, 2017). These factors may contribute to source-sink dynamics between the nature reserve and the estate, whereby the nature reserve supplements the population on the estate (Pulliam, 1988). If this were the case, then should the nature reserve be developed for future estates, the number and composition of species on the estate may change significantly. I would therefore support the continued presence of the nature reserve as an important contributor to avian diversity within the urban landscape mosaic (Threlfall *et al.*, 2017; Callaghan *et al.*, 2019; Villaseñor, Escobar and Hernández, 2021).

Appendix 5.1 Bird species common to both sites

Table S5.1.1: Bird species common to both Atlantic Beach Estate and Blaauwberg Nature Reserve, with both common names and scientific names provided.

Common name	Scientific name
African black swift	*Apus barbatus*
African goshawk	*Accipiter tachiro*
Alpine swift	*Tachymarptis melba*
Bar-throated apalis	*Apalis thoracica*
Bokmakierie	*Telophorus zeylonus*
Brimstone canary	*Crithagra sulphurata*
Brown-throated martin	*Riparia paludicola*
Cape bulbul	*Pycnonotus capensis*
Cape bunting	*Emberiza capensis*
Cape canary	*Serinus canicollis*
Cape grassbird	*Sphenoeacus afer*
Cape robin-chat	*Cossypha caffra*
Cape sparrow	*Passer melanurus*
Cape spurfowl	*Pternistis capensis*
Cape wagtail	*Motacilla capensis*
Cape weaver	*Ploceus capensis*
Cape white-eye	*Zosterops virens*
Chestnut vented warbler	*Sylvia subcaerulea*
Common house martin	*Delichon urbicum*
Common starling	*Sturnus vulgaris*
Egyptian goose	*Alopochen aegyptiaca*
Grey-backed cisticola	*Cisticola subruficapilla*
Helmeted guineafowl	*Numida meleagris*
Karoo prinia	*Prinia maculosa*
Karoo scrub robin	*Cerotrichas coryphoeus*
Laughing dove	*Spilopelia senegalensis*
Layard's warbler	*Sylvia layardi*
Levaillant's cisticola	*Cisticola tinniens*
Little swift	*Apus affinis*
Long-billed crombec	*Sylvietta rufescens*
Namaqua dove	*Oena capensis*
Pearl-breasted swallow	*Hirundo dimidiata*
Pied crow	*Corvus albus*
Red-eyed dove	*Streptopelia semitorquata*
Red-faced mousebird	*Urocolius indicus*

Reed cormorant	*Microcarbo africanus*
Ring-necked dove	*Streptopelia capicola*
Rock kestrel	*Falco rupicolus*
Rock martin	*Ptyonoprogne fuligula*
Southern boubou	*Laniarius ferrugineus*
Southern double-collared sunbird	*Cinnyris chalybeus*
Southern fiscal	*Lanius collaris*
Southern red bishop	*Euplectes orix*
Speckled mousebird	*Colius striatus*
Speckled pigeon	*Columba guinea*
Western cattle egret	*Bubulcus ibis*
White-backed mousebird	*Colius colius*
White-rumped swift	*Apus caffer*
White-throated canary	*Crithagra albogularis*
Yellow bishop	*Euplectes capensis*
Yellow canary	*Crithagra flaviventris*

Appendix 5.2 Station species richness

Table S5.2.1: The location of each station and the number of bird species found at each station.

Site	Station	X	Y	Species richness
ABE	A01 (1)	18.44467	-33.7368	25
ABE	A02 (2)	18.44565	-33.7348	29
ABE	A03 (3)	18.44872	-33.7363	25
ABE	A04 (4)	18.44932	-33.7338	32
ABE	B01 (5)	18.44444	-33.7405	26
ABE	B02 (6)	18.4462	-33.7403	24
ABE	B03 (7)	18.44652	-33.7421	25
ABE	B04 (8)	18.4465	-33.738	29
ABE	C01 (9)	18.44981	-33.7384	26
ABE	C02 (10)	18.45059	-33.7406	25
ABE	C03 (11)	18.45257	-33.7427	26
ABE	C04 (12)	18.45273	-33.7389	31
ABE	D01 (13)	18.44729	-33.7478	29
ABE	D02 (14)	18.44738	-33.7446	28
ABE	D03 (15)	18.44874	-33.7454	27
ABE	D04 (16)	18.45021	-33.748	25
ABE	E01 (17)	18.45183	-33.7509	32
ABE	E02 (18)	18.45227	-33.7523	32
ABE	E03 (19)	18.45291	-33.7469	41
ABE	E04 (20)	18.45304	-33.7505	31
BNR	F01 (21)	18.4497	-33.766	25
BNR	F02 (22)	18.44963	-33.764	21
BNR	F03 (23)	18.4534	-33.7643	26
BNR	F04 (24)	18.4537	-33.7622	19
BNR	G01 (25)	18.45072	-33.7699	25
BNR	G02 (26)	18.452	-33.7688	25
BNR	G03 (27)	18.45321	-33.7705	28
BNR	G04 (28)	18.45193	-33.7665	19
BNR	H01 (29)	18.45528	-33.7657	22
BNR	H02 (30)	18.45639	-33.7679	24
BNR	H03 (31)	18.45874	-33.7693	23
BNR	H04 (32)	18.45767	-33.7659	23
BNR	I01 (33)	18.45518	-33.7758	22
BNR	I02 (34)	18.45455	-33.7725	26
BNR	I03 (35)	18.45625	-33.7733	25
BNR	I04 (36)	18.4578	-33.7751	30
BNR	J01 (37)	18.4602	-33.7773	20
BNR	J02 (38)	18.46081	-33.7785	25
BNR	J03 (39)	18.45973	-33.7733	22
BNR	J04 (40)	18.46151	-33.7766	28

Appendix 5.3 Species richness parameter estimates

Table S5.3.1: Species richness parameter estimates for Atlantic Beach Estate.

Station	Distance to BNR (m)	NDVI	Water
A01 (1)	190	0.700637	0
A02 (2)	350	0.683829	0
A03 (3)	379	0.637173	0
A04 (4)	153	0.543042	1
B01 (5)	17	0.720187	0
B02 (6)	181	0.567869	0
B03 (7)	151	0.623397	0
B04 (8)	297	0.433816	0
C01 (9)	288	0.637046	0
C02 (10)	232	0.565273	0
C03 (11)	137	0.518508	0
C04 (12)	84	0.583437	0
D01 (13)	11	0.573284	0
D02 (14)	152	0.722673	0
D03 (15)	261	0.389011	0
D04 (16)	158	0.592058	0
E01 (17)	70	0.504813	0
E02 (18)	14	0.366447	0
E03 (19)	93	0.744136	1
E04 (20)	7	0.392478	0

Table S5.3.2: Species richness parameters for Blaauwberg Nature Reserve.

Station	Distance to settlement (m)	Distance to roads (m)	NDVI
F01 (21)	1512.889	395.099	0.535484
F02 (22)	1293.084	469.798	0.559267
F03 (23)	1308.09	597.993	0.677123
F04 (24)	1082.733	476.029	0.544035
G01 (25)	1116.252	329.632	0.571507
G02 (26)	1193.832	482.205	0.402321
G03 (27)	988.859	520.898	0.51011
G04 (28)	1445.164	568.464	0.453732
H01 (29)	1484.666	507.167	0.538267
H02 (30)	1255.99	516.145	0.50431
H03 (31)	1139.803	384.311	0.434031
H04 (32)	1494.867	313.582	0.576948
I01 (33)	374.274	484.284	0.346702
I02 (34)	750.288	556.21	0.426881
I03 (35)	662.648	672.396	0.724457
I04 (36)	507.146	733.976	0.504182
J01 (37)	495.587	634.167	0.466558
J02 (38)	509.928	642.318	0.475177
J03 (39)	768.452	488.501	0.440404
J04 (40)	636.618	493.584	0.335471

Appendix 5.4 Functional groups

Table 5.4.1: Functional groups for all bird species found on Atlantic Beach Estate and/or Blaauwberg Nature Reserve.

	Granivores	Grazers	Raptors	Scavengers	Ecosystem engineers	Seed dispersers	Pollinators	Nutrient depositors	Insectivores
African black swift	0	0	0	0	1	0	0	0	1
African darter	0	0	1	0	0	0	0	1	0
African goshawk	0	0	1	0	0	0	0	0	0
African hoopoe	0	0	0	0	0	0	0	0	1
Alpine swift	0	0	0	0	1	0	0	0	1
Bar throated apalis	0	0	0	0	0	0	0	0	1
Barn swallow	0	1	0	0	0	0	0	0	1
Black-crowned night-heron	0	0	1	0	0	0	0	0	0
Black-headed heron	0	0	1	0	0	0	0	0	1
Black-shouldered kite	0	0	1	0	0	0	0	0	0
Blacksmith lapwing	0	0	0	0	0	0	0	1	1
Bokmakierie	0	0	0	0	0	1	0	0	1
Brimstone canary	1	1	0	0	0	1	1	0	0
Brown throated martin	0	0	0	0	1	0	0	1	1
Cape bulbul	0	0	0	0	0	1	1	0	1
Cape bunting	1	1	0	0	0	1	0	0	0
Cape canary	1	1	0	0	0	1	0	0	0
Cape grassbird	0	0	0	0	0	0	0	0	1
Cape robin-chat	0	0	0	0	0	1	0	0	1
Cape sparrow	1	1	0	0	0	1	1	0	1
Cape spurfowl	0	1	0	0	0	1	0	0	1
Cape sugarbird	0	0	0	0	0	0	1	0	0
Cape turtle dove	1	0	0	0	0	0	1	0	0
Cape wagtail	0	0	0	0	0	0	0	1	1
Cape weaver	0	1	0	0	0	0	1	0	1
Cape white-eye	0	0	0	0	0	1	1	0	1
Cattle egret	0	0	0	0	0	0	0	0	1
Chestnut vented tit-babbler	0	0	0	0	0	1	1	0	1
Common fiscal	0	0	1	1	0	0	0	0	1
Common house martin	0	0	0	0	0	0	0	0	1
Common moorhen	0	1	0	1	0	0	0	0	1
Common starling	0	0	0	1	0	0	1	0	1
Common waxbill	1	1	0	0	0	0	0	0	1
Dusky sunbird	0	0	0	0	0	0	1	0	0
Egyptian goose	1	1	0	0	0	0	0	1	0
European bee-eater	0	0	0	0	0	0	0	0	1
Greater striped swallow	0	0	0	0	1	0	0	0	1
Grey heron	0	0	1	1	0	0	0	1	0
Grey-backed cisticola	0	0	0	0	0	0	0	0	1
Grey-winged francolin	0	1	0	0	0	0	0	0	1

Hadeda ibis	0	0	0	0	0	0	0	0	1
Helmeted guineafowl	0	1	0	0	0	0	0	0	1
House sparrow	1	1	0	0	0	1	1	0	1
Jackal buzzard	0	0	1	1	0	0	0	0	0
Karoo prinia	0	0	0	0	0	0	0	0	1
Karoo scrub-robin	0	0	0	0	0	1	0	0	1
Laughing dove	1	0	0	0	0	1	0	0	0
Layard's tit-babbler	0	0	0	0	0	1	0	0	1
Levaillant's cisticola	0	0	0	0	0	0	0	1	1
Little bittern	0	0	1	0	0	0	0	0	0
Little egret	0	0	1	0	0	0	0	1	0
Little swift	0	0	0	0	1	0	0	0	1
Long billed crombec	0	0	0	0	0	1	1	0	1
Malachite sunbird	0	0	0	0	0	0	1	0	0
Namaqua dove	1	0	0	0	0	0	0	0	0
Olive thrush	0	0	0	0	0	1	0	0	1
Pearl-breasted swallow	0	0	0	0	0	0	0	0	1
Pied crow	0	0	1	1	0	1	1	0	1
Pin-tailed whydah	1	0	0	0	0	0	0	0	0
Purple heron	0	0	1	0	0	0	0	0	0
Red bishop	1	1	0	0	0	0	0	0	0
Red eyed dove	1	0	0	0	0	0	0	0	0
Red faced mousebird	0	0	0	0	0	1	1	0	0
Red-knobbed coot	0	1	0	1	0	0	0	1	0
Red-winged starling	0	0	1	1	0	1	1	0	0
Reed cormorant	0	0	1	0	0	0	0	1	0
Rock kestrel	0	0	1	0	0	0	0	0	0
Rock martin	0	0	0	0	1	0	0	0	1
Southern boubou	0	1	1	0	0	0	1	0	1
Southern double-collared sunbird	0	0	0	0	0	0	1	0	0
Southern masked weaver	1	0	0	0	0	0	1	0	0
Speckled mousebird	0	1	0	0	0	1	1	0	0
Speckled pigeon	1	1	0	0	0	0	0	0	0
Spotted thick-knee	0	0	0	0	0	0	0	0	1
Steppe buzzard	0	0	1	0	0	0	0	0	1
Water thick-knee	0	0	1	0	0	0	0	0	1
White backed mousebird	0	1	0	0	0	1	1	0	0
White-rumped swift	0	0	0	0	1	0	0	0	1
White-throated canary	1	1	0	0	0	1	0	0	0
White-throated swallow	0	0	0	0	1	0	0	0	1
Yellow bishop	1	0	0	0	0	0	0	0	0
Yellow canary	1	1	0	0	0	0	1	0	0
Yellow-billed kite	0	0	1	1	0	0	0	0	0

CHAPTER 6: Synthesis

Background and summary of findings

The human population is continuing to expand, and as a result, so too is the human footprint. The burgeoning population requires increasing amounts of natural resources and land for a variety of activities including residential housing. Private estates are an elite form of residential housing and in highly unequal countries where violent crime is systemic provide a form of geographical escapism (Lemanski, 2004; Landman and Badenhorst, 2012). In an attempt to rebrand away from elitism, and in the face of increasing environmental awareness, many private estates have rebranded as eco-estate and they are increasingly dramatically in number (Ballard and Jones, 2011; Sherriff-Shüping, 2015). Despite their increasing prevalence, no formal definition exists for eco-estates allowing them to make bold claims about their contribution to environmental sustainability and conservation with little to no accountability (Thambu, 2007). Currently, little is known about the impacts of eco-estates on wildlife, particularly when compared to natural land, as much research has focused on comparing eco-estates to previously transformed land, such as agricultural or urban land (Grey-Ross, Downs and Kirkman, 2009; Alexander *et al.*, 2019a, 2019b). This study seeks to address this gap in the literature by comparing Atlantic Beach Estate, a high security eco-estate located 25 km north of Cape Town to a control site, Blaauwberg Nature Reserve, which borders the estate, and out of which the estate was cleaved.

As noted throughout this thesis, eco-estates vary in their suitability for different taxa and species. With reference to small mammal diversity (Chapter 3), the estate had the same number of species as the reserve, though this included exotic species closely associated with humans (i.e., the house rat (*Rattus rattus*)). In addition, the estate did not support the vulnerable white-tailed rat (*Mystromys albicaudatus*). On balance, the estate maintained a similar species composition to that of the nature reserve and had better measures of evenness and diversity. By contrast medium sized mammal species composition varied markedly between the estate and the reserve with the former not supporting multiple indigenous medium sized mammals found within the reserve (Chapter 4). Though the estate had a similar number of species, many of these were domestic animals, and one, the springbok (*Antidorcas marsupialis*), is an introduced, extralimital species. Given the destructive tendencies of companion animals, notably domestic cats (*Felis catus*), the relative impermeability of the fence separating the estate and the reserve is likely beneficial for those species residing in the reserve. In terms of birds (Chapter 5), the estate can support a much higher bird diversity than the reserve. In addition to supporting almost all the species found in the reserve, the estate was able to support many fynbos-endemic species not found in the reserve, as well as species closely associated with permanent water. The presence of the eco-estate does not appear to have negatively impacted the bird community as the additional resources provided by the estate allow both urban exploiters and urban tolerators/avoiders to persist. In summary, the estate scores averagely for small mammals, poorly for medium-sized mammals and well for birds.

Improving conditions for wildlife on the estate

One of the premises of eco-estates is the creation of an ecosystem where both wildlife and humans can thrive. This dissertation seeks, in part, to address some of the challenges faced by wildlife on the estate and provide ways in which these challenges can be overcome. One of the most concerning issues facing small mammals and birds on the reserve is the large number of domestic cats detected ubiquitously across the estate. Domestic cats are unequivocally detrimental to local ecosystems (van Heezik *et al.*, 2010; Loss, Will and Marra, 2013; Loss and Marra, 2017). One must assume domestic cats are similarly destructive on the estate, though this impact may be mitigated by the supplementary resources provided by the estate because, paradoxically, small mammals and birds appear to be persisting relatively well on the estate. However, domestic cats are a contentious issue within the estate, with advocates arguing strongly for and against their presence on communal estate grounds, and some going as far as to suggest cats should be banned entirely from the estate (Nattrass and O'Riain, 2020). Management has responded by seeking resident's perspectives on the issues, but are yet to act on the responses they have received (Nattrass and O'Riain, 2020) and as a result, domestic cat numbers on communal areas of the estate have been high for a number of years (van Wyk, 2017) with the assumed associated impacts on local wildlife (Seymour *et al.*, 2020). Lessening the impact of domestic cats would require enforcing rules already in place – requiring domestic cats to be confined to owners properties and that each outdoor-going cat be fitted with a bell (Atlantic Beach Homeowners Association, 2013), both of which will reduce domestic cat predation on wildlife (Willson, Okunlola and Novak, 2015). Some owners have taken the initiative by installing "catios" which raise the perimeter fence around their individual properties, effectively containing cats but allowing them access to the outdoors (Nattrass and O'Riain, 2020). A recent study revealed that domestic cats catch 5.56 times more prey than they bring home suggesting cat owners may be unaware of the damage their pets are causing when they roam in public open natural spaces (Seymour *et al.*, 2020). Increasing awareness of the impact of cats on the "eco" of estates may encourage cat owners to invest in structures that retain them on their private property.

Small mammals, and to some degree birds, highlighted the change in species composition as one moved from the periphery of the estate towards the centre, with patches closer to the perimeter having a species composition more similar to the nature reserve. Increasing the number of patches of natural land and improving patch connectivity would likely homogenize the species composition between the nature reserve/edge of the estate and the centre of the estate (Ramesh, Kalle and Downs, 2016). This would need to occur in conjunction with a targeted attack on human commensal species (particularly the house rat), which in addition to damaging human infrastructure (Almeida, Corrigan and Sarno, 2013) and being vectors of disease (Meerburg, Singleton and Kijlstra, 2009), can pose significant threats to local rodent and bird populations (Witmer and Shiels, 2018).

The Atlantic Beach Homeowners Association has published an approved plant list guiding residents as to the plant species they can plant in their respective gardens (see Atlantic Beach Homeowners Association (2017)). This list contains mainly indigenous fynbos species, but also a multitude of non-native species from across South Africa. While visually appealing and potentially more familiar to residents, these species are not necessarily in the best interest of local wildlife or biodiversity generally. A suite of floral species are generally planted by people in urban and peri-urban areas across South Africa (and indeed the world). The result can be biological homogenization which, while potentially bolstering local species richness, may result in a decrease in global biodiversity (McKinney, 2006). In addition, non-native species have the potential to become invasive which represents a large threat to biodiversity globally (Simberloff, 2015). Non-native species should be removed, and only indigenous species planted (Alexander *et al.*, 2021).

There is no question that the large swathes of fairways and greens implicit in any golf course create a simpler ecosystem, which may be home to a different suite of species than that found in nearby natural patches, particularly in the highly diverse Cape Floral Kingdom (Myers *et al.*, 2000). Thus the golf course may superficially increase species richness, because it facilitates urban exploiters such as the hadeda ibis and blacksmith lapwing which are both widely distributed across South Africa, and are increasing their range as human developments expand (Hockey, 2003; Hockey and Midgley, 2009; Duckworth, Altwegg and Guo, 2010). By contrast fynbos specialist species are largely limited to natural patches and thus limiting the extent of the golf-playing area, and increasing the number and connectivity of natural patches to create “naturalistic” golf courses, may have better served the combined interests of golfers and wildlife alike (Terman, 1997; Tanner and Gange, 2005; Colding and Folke, 2009; Alexander *et al.*, 2019a, 2021).

Guidelines for choosing eco-estate developments

Atlantic Beach Estate is a single eco-estate, which has already been constructed, yet there are important principles which can be extrapolated to inform future eco-estate planning. These principles are based on the conditions under which eco-estates could be approved or not (Figure 6.1). I suggest three questions to consider, among a multitude of possible others, but which are particularly relevant given the findings of this dissertation.

The first question is: do threatened species live in the area which is proposed for development (see https://www.iucnredlist.org/)? Should threatened species persist, particularly if these species are habitat specialists, it is unlikely than an eco-estate will adequately support such species (Devictor, Julliard and Jiguet, 2008). If no threatened species, or those with specialist habitat requirements, exist one can progress to the second question:

Are there large mammals in the area? In particular, do these large mammals pose a threat to humans, and if not, could they be managed as part of a larger metapopulation? These questions recognize that some large mammals, such as lion and elephant, generally do not persist well in close contact with humans and pose a significant risk to human lives and livelihoods (Nyhus, 2016). Despite their best intention to convince us otherwise, eco-estates are fundamentally concerned with housing humans, and as a result, human wellbeing is likely to be placed above that of wildlife. Furthermore, eco-estates are in large part concerned with the security of residents and thus are heavily fenced, severely restricting the movement of medium-large mammals. In order to maintain healthy genetic diversity, and prevent the deleterious effects of inbreeding (Charlesworth and Charlesworth, 1987), large mammals contained within an eco-estate would need to be managed as part of a larger metapopulation. If a proposed site fails in either of those two respects, I would consider it unsuitable, if not, it passes on to the third and final criterion.

The third question concerns the current state of the land proposed for development: is the land natural, or previously transformed (Alexander *et al.*, 2021)? If the land satisfies all the other afore-mentioned requirements for eco-estate construction, but exists on natural land, one should think carefully about construction an eco-estate. Locations which fall into this category have been termed "maybe". Eco-estates located on previously transformed agricultural land may increase wildlife diversity and abundance (Grey-Ross, Downs and Kirkman, 2009; Alexander *et al.*, 2019b). Additionally, transforming urban areas by increasing green spaces in these areas may increase species and functional diversity (McPherson, Brown and Downs, 2016; Patterson, Kalle and Downs, 2018), and therefore plots of land in previously transformed habitats should be considered first when deciding where to construct an estate.

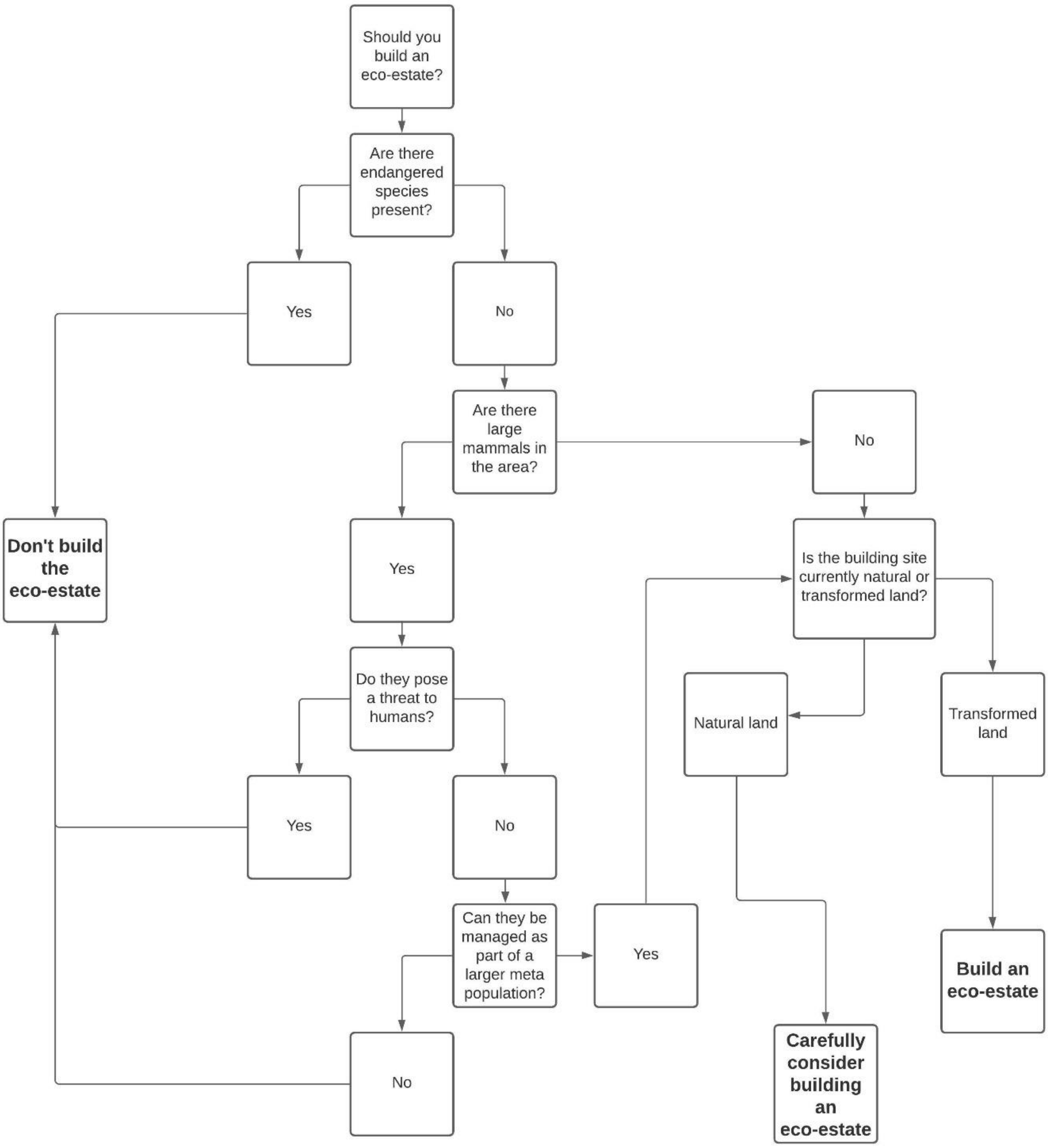


Figure 6.1: Flow chart outlining possible qualifiers and disqualifiers when considering constructing an eco-estate.

Considerations for pre-existing eco-estates and enforcement

In addition to the above-mentioned design features and changes to the estate, other lessons gleaned from this study can help improve the current status of wildlife in existing eco-estates. The presence of water can significantly increase bird species richness (Alexander *et al.*, 2019a, 2019b). Depending on the surrounding landscape, permanent water bodies can bolster species richness without negatively impacting those species naturally occurring in the surrounding area (McKinney, Raposa and Cournoyer, 2011). Even small bird baths can help bolster bird species richness in an area (Coetzee, Barnard and Pauw, 2018). Additionally, the provision of supplementary food resources (e.g., sugar water for nectarivorous species) may increase species richness (Davis, Major and Taylor, 2015; Coetzee, Barnard and Pauw, 2018, 2021) although not without some health risks to birds (Murray *et al.*, 2016).

Currently no formal definition of the term “eco-estate” exists, and estates are free to make any claims they wish around their environmental friendliness. Mistry and Spocter (2020) suggest five categories for eco-estates and eco-friendly estates in South Africa, depending on their level of environmental friendliness across 13 eco-practices. Using the terms “eco-estate”, “eco-neighbour estate”, “eco-friendly estate”, “eco-conscious estate” and “eco-orientated resort” as suggested by Mistry and Spocter (2020) would allow estates to be differentiated on the basis of their commitment to the environment. Estates themselves would be aware of what constitutes the gold standard for environmental custodianship, and homeowners would be better able to make informed decisions about where to live based on objective standards as opposed to the greenwashing that most “eco-estates” present to potential buyers. Atlantic Beach Estate might be best considered an “eco-orientated estate”.

Conclusions

The issues surrounding domestic cats in Atlantic Beach Estate potentially serves as a useful proxy for understanding the underlying issues within eco-estates generally. While domestic cats are known to be devastating predators and are not permitted to leave their owners premises and are required to wear a bell, these conditions are not enforced. It is possible that leniency is to avoid conflict between management and residents which has at times been severe (Nattrass, 2019). When it comes down to a choice between humans and wildlife, even in an eco-estate, human comfort and convenience is generally considered first. For some species, particularly small mammals and birds, human desires may coincide with wildlife needs and both can likely persist, while for other species (such as medium/large mammals), coexistence is potentially less plausible, and would require active human management to maintain a genetically healthy population. It is thus perhaps best to avoid considering eco-estates as additional land for wildlife, but rather curated nature on which we are pleasantly surprised to find select wildlife. Maybe the best hope for eco-estates in terms of meaningful wildlife conservation is if they act as refuges for wildlife suffering from persecution elsewhere, for the imposing fences which protect humans could equally well protect wildlife.

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