

**Aspects of the ecology of African woolly-necked
storks (*Ciconia microscelis*) in an anthropogenic
changing landscape in KwaZulu-Natal, South
Africa**

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ABSTRACT

Urbanisation is the fastest-growing forms of anthropogenic land use change and a major threat to biodiversity worldwide. However, despite the negative impacts of urbanisation on native species, some species persist in urbanised environments and this thesis aimed to examine one such species, the African woolly-necked stork (*Ciconia microscelis*). African woolly-necked storks have recently colonised urbanised environments in KwaZulu-Natal, South Africa, and are now common in suburban areas in particular. Despite its proximity to human settlements and recent high abundance in suburban areas, knowledge of the African woolly-necked stork remains poorly documented in South Africa. Therefore, this thesis aimed to investigate the aspects of ecology of African woolly-necked storks within the suburban landscape to determine what factors facilitate their ability to persist in these environments.

Firstly, I assessed the long-term trends in occupancy, colonisation and extinction of African woolly-necked storks as a function of change in land cover across KwaZulu-Natal Province, South Africa. This was accomplished by applying dynamic occupancy models to 26 years (1992-2017) of citizen science presence/absence data from Coordinated Waterbird Counts in South Africa. African woolly-necked stork wetland occupancy was relatively stable ($\psi = 0.37-0.39$) across years. However, they rapidly extended their distribution range to urbanised environments, becoming common in man-made wetlands. Overall, this study found that the increased area of anthropogenic areas led to an increase in the probability of wetland colonisation by African woolly-necked storks.

Secondly, I investigated the foraging opportunities that might be responsible for the recent colonisation of urbanised environment by African woolly-necked storks. I found that a significant number of householders (71%) deliberately fed African woolly-necked storks daily throughout the year and the majority provided meat while others fed inappropriate

food such as bread. Furthermore, I found that, African woolly-necked storks were relatively habituated in urban areas of KwaZulu-Natal, with some even feeding from hand and others going inside homes to find the supplemental food. These results showed that the African woolly-necked stork is successfully utilising and exploiting anthropogenic food – a novel behaviour for this species.

Thirdly, given that the selection of appropriate nest sites has major implications on reproduction success and survival of urban bird species, I was interested to determine if African woolly-necked storks bred in urbanised areas and, if so, which features of the nest site and surrounding habitat influenced their occupancy. I found 30 African woolly-necked stork nests in suburban areas of KwaZulu-Natal. African woolly-necked storks have successfully established breeding sites in suburban areas (mostly in domestic gardens), especially near swimming pools, while exotic pine (*Pinus elliottii*) and eucalyptus (*Eucalyptus spp.*) trees were the most preferred trees. Anthropogenic structures were also used as nesting sites suggesting a nesting behaviour shift.

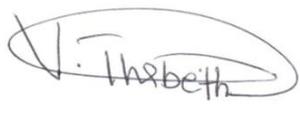
Lastly, after acquiring evidence that African woolly-necked storks successfully utilise anthropogenic food and have established a breeding population in urban areas, I was interested to know what food they provisioned to their nestlings. Furthermore, I investigated the breeding behaviour of African woolly-necked storks using direct observations and infrared camera traps during three breeding seasons (2015-2017). Although anthropogenic food was provided to nestlings, African woolly-necked storks provisioned their nestlings predominantly with natural food, primarily amphibians, particularly guttural toads (*Amietophrynus gutturalis*). African woolly-necked storks consistently reoccupied most nest sites across study years since initial discovery, suggesting that this population was at least stable. For the first time, I documented evidence of cooperative breeding where more than two adults provided care to a single nest.

This thesis showed that African woolly-necked storks have the behavioural flexibility to take advantage of anthropogenic resources in suburban landscapes. Their behavioural flexibility in habitat selection, and tolerance to humans allows African woolly-necked storks to live in suburban areas, and other urbanised areas, where they were once absent or uncommon. This is the first study on African woolly-necked storks in Africa, which thus fills a significant knowledge gap.

PREFACE

The data described in this thesis were collected in Pietermaritzburg and Durban, Republic of South Africa from February 2015 to November 2017. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Colleen T. Downs.

This thesis, submitted for the Doctoral degree of Science in the College of Agriculture, Science and Engineering, University of KwaZulu-Natal, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.



Vuyisile Thabethe

November 2018

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



.....

Professor Colleen T. Downs

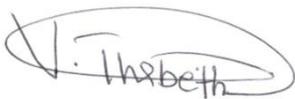
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DECLARATION 1 - PLAGIARISM

I, Vuyisile Thabethe, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
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DECLARATION 2 - PUBLICATIONS

DETAIL OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication 1 (Submitted to Journal of Ornithology)

V Thabethe and CT Downs. Long-term trends (1992-2017) in occupancy, colonisation and decreased local extinction of African woolly-necked storks in KwaZulu-Natal, South Africa

Author contributions:

VT and CTD conceived paper. VT collected, analysed data and wrote the paper. CTD reviewed the manuscript and provided valuable comments.

Publication 2 (Published in Urban Ecosystems)

V Thabethe and CT Downs (2018). Citizen science reveals widespread supplementary feeding of African woolly-necked storks in suburban areas of KwaZulu-Natal South Africa. Urban Ecosystem 21:965–973

Author contributions:

VT and CTD conceived paper. VT collected, analysed data and wrote the paper. CTD reviewed the manuscript and provided valuable comments.

Publication 3 (Submitted to Urban Ecosystems)

V Thabethe and CT Downs. Nest site selection of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa, and implications for its requirements

Author contributions:

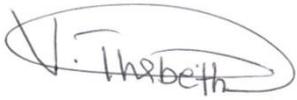
VT and CTD conceived paper. VT collected, analysed data and wrote the paper. CTD reviewed the manuscript and provided valuable comments.

Publication 4 (Formatted for submission to Journal of Ornithology)

V Thabethe, S McPherson and CT Downs. Nestling provision and breeding behaviours of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa

Author contributions:

VT, SM, and CTD conceived paper. VT collected, analysed data and wrote the paper. CTD reviewed the manuscript and provided valuable comments.

A handwritten signature in black ink, appearing to read 'V. Thabethe', is enclosed within a hand-drawn oval. Below the signature is a solid horizontal line.

Signed:

Vuyisile Thabethe

November 2018

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CHAPTER 1

Introduction

1.1 Urbanisation

Urbanisation, the most common cause of habitat degradation, is rapidly expanding throughout the globe (Marzluff 2001, McKinney 2002, Minias 2016). Urban areas are presently expanding at a faster rate than any other land use type (McKinney 2006, Seto et al. 2012, Wang et al. 2015). By 2050, the percentage of the world's population living in urban areas is projected to increase from the current 54% to approximately 70% (Cohen 2006, Seto et al. 2012, United Nations 2014, Minias 2016). Urban areas generally comprise a heterogeneous habitat mosaic containing clusters of high- and low-density buildings, intensively-managed green spaces, natural habitat remnants and linear features such as roads, rivers and railway lines (McKinney 2006, Croci et al. 2008).

The process of urbanisation has diverse effects including fragmentation, isolation and degradation of natural habitats (Marzluff and Ewing 2001). Additionally, urban areas are characterized by several transformed environmental factors such as increased levels of chemical, noise and light pollution (Slabbekoorn et al. 2007, Dominoni et al. 2013). These novel pressures make urban areas challenging environments for wildlife to survive in (Lowry et al. 2012). Accordingly, urbanisation is considered as a major wildlife threat throughout the world (Marzluff and Ewing 2001, McKinney 2006, Biamonte et al. 2011). Despite the many challenges of living in urban environments, some native avian persist in urbanised environments (Marzluff et al. 2001, Francois et al. 2008, Moller 2009, Martin et al. 2010, Aronson et al. 2014, Seress and Liker 2015, Gilbert et al. 2016, Jagiello et al. 2018). Therefore, the need to understand how wildlife responds to the impacts of anthropogenic development is becoming increasingly important.

1.2 Urban birds

Several urban studies have assessed the effects of urbanisation on biodiversity across rural-urban gradients/mosaics (Shochat et al. 2010, Aronson et al. 2014). Generally, compared to adjacent natural areas, bird communities in urban areas are characterized by low species richness and diversity to the advantage of a few broadly adapted species that may be particularly abundant (Biamonte et al. 2011, Henderson 2015). Exotic species generally thrive in the novel urban environment, while many native species avoid it (Lowry et al. 2012). The loss of native species and the subsequent increase in non-native species often leads to biotic homogenization (Clergeau et al. 2006, Shochat et al. 2010). Generally, the birds shown to decline in areas of urbanisation are specialist species and the reduction is mainly due to unsuitable habitat provided by urban areas (Crocì et al. 2008). For example, Pauw and Louw (2012) reported the decline in specialist species such as the malachite sunbird (*Nectarinia famosa*) associated with metropolitan areas. Whereas species subsisting in urbanised environments are mainly generalist (particularly omnivores) thus able to exploit anthropogenic food (Kark et al. 2007, Moller 2009, Shochat et al. 2010, Barnagaud et al. 2011, Duckworth and Altwegg 2014). Avian species that exhibit such traits and are common to urban areas throughout the world include sparrows (*Passer domesticus*), European starlings (*Sturnus vulgaris*) and rock doves (*Columbia livia*) (Winiarski et al. 2017).

Species richness tends to decrease within the extreme urbanisation found in city and town cores (Marzluff 2001, Clergeau et al. 2006). More intense Urbanisation decreases the amount of resources available and removes a substantial amount of land from primary production which is permanently replaced with pavement and structures (McKinney 2002, Kark et al. 2007, Crocì et al. 2008). At more moderate levels of urbanisation (i.e. suburban areas), a mosaic of potential habitat can be found, and here responses to variation differs among taxa (Galbraith et al. 2015). Moderate levels of Urbanisation lead to increased habitat

heterogeneity through increase in ornamental vegetation, water sources, primary productivity, and the amount of edge between habitats (Faeth et al. 2005, Marzluff 2001). As a result, moderate levels of Urbanisation critically increase the abundance of resources that can be exploited by native birds which also attracts widely ranging species, leading to overall high species diversity (Francois 2008, Gilbert et al. 2016). Indeed, a recent global study showed that 20% of all bird species in the world occurs in urban areas (Aronson et al. 2014), suggesting that urbanised environments still have significant conservation value despite the threat to biodiversity that urbanisation represents (Aronson et al. 2014).

Many studies suggest that certain combination of traits or behavioral flexibility are required to enable species to persist in urbanised environment (Ditchkoff et al. 2006, Kark et al. 2007, Lowry et al. 2012). The ability to habituate to the presence of humans is one of the key traits suggested as being essential for successful adaptation to the urbanised environments (Soh et al. 2002, Ishtiaq et al. 2004, Vaghela et al. 2015, Wang et al. 2015, Kopij 2017). Birds that are habituated to humans can exploit anthropogenic resources for both breeding and foraging (Blanco 1997, Bochenski 2005, Calle et al. 2011, Gillanders et al. 2017).

Food source is considered as a main factor for the success of birds in urbanised environments (Ewen et al. 2015, Djerdali et al. 2016). Urban areas offer a variety of natural, intentional or incidental anthropogenic food for wild birds. Natural food resources may be in the form of an increase in naturally occurring preys such as invertebrates, amphibians and reptiles from artificial water bodies, open green spaces, agricultural fields (Orros et al. 2015). The simple structure of suburban irrigated lawns has been suggested as a positive feature that may increase foraging success (Singh and Downs 2016).

In addition to an increase in natural food resources, supplementary food is another important resource utilised by birds in urban and suburban areas (Jones and Reynolds 2008, Orros and Fellowes 2015, Hanmer et al. 2016, Reynolds et al. 2017). Indisputably,

supplementary feeding provides an extremely important reliable food resource to many suburban birds in the most part of the world (Howard and Jones 2004, Cox and Gaston 2016). Even so, supplementary feeding of birds is now seen as a necessary means for facilitating wild birds in urbanised areas and has also been promoted as one of ten approaches for the enhancement of wild bird abundance and diversity in suburban areas (Ewen et al. 2015, González et al. 2006).

The provision of supplementary food generally leads to advances in lay dates, increase in clutch size, improved nestling physical conditions and subsequently increased breeding success (Lowry et al. 2012, Perrig et al. 2014, Hilgartner, Djerdali et al., 2016, Cereghetti 2017). Therefore, some species are abundant and widely distributed in their range owing to supplementary feeding for example, Australian magpies (*Gymnorhina tibicen*) (O’Leary and Jones 2006) and red kite (*Milvus milvus*) (Orros and Fellowes 2014, 2015b). Globally, landfills sites have become an important food resource within/surrounding urban habitats for birds (Bochenski and Jerzak 2006, Kruszyk and Ciach 2010, Gilbert et al. 2016). Corvid populations are continuing to expand throughout the world, almost certainly owing to the abundance of anthropogenic foods (Marzluff et al. 2001, Heiss et al. 2009). Foraging at landfill sites has been implicated in species range changes and increased abundance (Kruszyk and Ciach 2010).

While feeding is likely to benefit the survival of certain species, concerns over potential negative effects of the practice have been raised (Wilcoxon 2015, Meyrier et al 2017). In a study conducted by Heiss et al. (2009), American crow’s (*Corvus brachyrhynchos*) nestlings reared in an urban landscape exhibited nutritional limitations due to the high levels of anthropogenic food items in their diet. Another concern is the possibility that some species may become dependent on human-providing food and enhancement of introduced species (Ishigame and Baxter 2007, Plummer et al. 2015). Furthermore, the process of supplementary feeding

may facilitate the transmission of disease, which can lead to population declines (Robinson et al. 2010).

Compared with rural/natural sites urban habitats are characterized by increased abundance of nesting sites (White et al. 2005, Wang et al. 2015). These include anthropogenic structures and exotic trees. Consequently, several bird species nest on both anthropogenic structures and exotic trees in urban areas (Stout and Rosenfield 2010). For example, white storks (*Ciconia ciconia*) (Moreira et al. 2018), white ibis (*Accipiter melanoleucus*) and yellow-legged gulls (*Larus michahellis*) (Soldatini et al. 2008), (Martin et al. 2010) build their nest on anthropogenic structures. While hadeda ibis (*Bostrychia hagedash*) (Singh and Downs 2016) and sparrow hawks (*Accipiter melanoleucus*) (Curtis et al. 2007) are utilising exotic trees for both nesting and roosting. It is clear that some urban environments provide many resources that can benefit certain bird species positively.

Despite the existence and persistence of some avian species in the urban environment throughout the globe, most studies on urban birds have been mainly conducted in the Northern Hemisphere, especially North America and Europe. On the other hand, there are only few studies in other continents such as South America and Africa. This has left the Southern Hemisphere underrepresented within the urban ecological literature. Studies of urban avifauna at these understudied continents are however necessary if we are to obtain a global perspective of urban ecology (Marzluff 2001). Avian populations within urbanised areas provide unique situations in which to undertake research on how species adapt and survive in novel environments to be addressed.

1.3 Waterbirds in cities

Globally, waterbirds populations are declining regardless of their importance as indicators of ecosystem health (Wetlands International 2014, Herbst 2015, Dini and Everard 2016, Matchett

and Fleskes 2017). Studies on population trends suggest that the main cause of decline is the increased loss of wetlands through anthropogenic land-uses (Kentula et al. 2004, Glisson et al. 2017, Li et al. 2014). Concerns over declines of waterbirds have promoted variety of conservation plans, many of which promote protection, expansion and creation of wetlands within an urban landscape (Breininger and Smith 1990, Harebottle et al. 2012). As a result, many wetlands are protected by international conservation treaties such as Ramsar Convention (Kleijn et al. 2014) and many artificial wetlands have been created in urban areas throughout the globe (Valente et al. 2011, Murray et al. 2013). Studies show that a wide range of waterbirds successfully utilise these created wetlands (Breininger and Smith 1990, Traut and Hostetler 2003, Scholte 2006, Sundar 2003, Murray et al. 2013, Duckworth and Altwegg 2014, Andrade et al. 2018, Jia et al. 2018). Waterbird species adapted to artificial wetlands generally have much higher population densities than in rural/natural populations (Marzluff et al. 2001, Van den Bossche et al. 2002, Moller 2009, Martin et al. 2010, Conover 2011, Gilbert et al. 2016).

Storks have had a traditional reputation of being sensitive to human proximity and disturbance (Sundar 2003, Bochenski and Jerzak 2006, Ezaki and Ohsako 2012, Anila et al. 2016). However, although fragmented habitats usually are less productive for stork species (Djerdali et al. 2016), some stork species today are found living in close proximity to humans in suburban and urban settings in many parts of the globe. For example, white storks (Tortosa et al. 2002, Kruszyk and Ciach 2010, Cheriak et al. 2014), black stork (*Ephippiorhynchus asiaticus*) (Sundar 2003), wood stork (*Mycteria Americana*) (Depkin et al. 1992), marabou stork (*Leptoptilos crumeniferus*) (Pomeroy and Kibuule 2017), Abdim's stork (*Ciconia abdimii*) (Falk et al. 2006) and Asian woolly-necked storks (*Ciconia episcopus*) (Vaghela et al. 2015, Greeshma et al. 2018) are now nesting in cities or densely populated areas throughout their respective range.

Land fill sites provide a significant, concentrated and predictable food supply especially needed during the cold winter months (Bochenski and Jerzak 2006). White and marabou storks have taken advantage of these new foraging areas in urbanised environments and this has increased their breeding success. As reported by Vergara et al. 2010 and Vaghela et al. 2015, white and Asian woolly-necked storks nest on artificial structures such as roofs and electric poles. In urbanised settings where suitable nest trees are often rare, this adaptation certainly gives them a competitive advantage. It is worth to note that these behaviours are not necessarily common to every species of stork. In contrast to the extensive knowledge on the ecology of urban storks in northern hemisphere little is known about their southern hemisphere counterparts. Therefore, more on urban storks are needed in southern hemisphere, particularly in Africa some stork species have colonised urban environments.

1.4 African woolly-necked storks

The African woolly-necked stork (*Ciconia microscelis*) is a large wading bird which belongs to the *Ciconia* family and indigenous to Africa. Previously, the *C. episcopus* and *C. microscelis* were previously lumped as *C. episcopus*. However, the African population has been recently split from its Asian counterpart *C. episcopus* and assigned a specific status as African woolly-necked stork *C. microscelis* by del Hoyo et al. (2014). The African woolly-necked stork is easily recognised by its fluffy white neck with the rest of the plumage black. It has a wide distribution across Africa from northern (e.g. Sudan) to sub-Saharan Africa (e.g. South Africa) (Brown et al. 1982, del Hoyo et al. 1992, del Hoyo et al. 2018) (Fig. 1.1). The natural habitats are generally wetlands and mudflats (Cyrus and Robson 1980). When not breeding the species is normally seen solitarily or in pairs, and sometimes in small flocks (Brown et al. 1982), although it may collect in flocks of several hundred (del Hoyo et al. 1992) on migration (Brown et al. 1982). Traditionally, this stork occurred along banks of river, swamps, streams, lakes,

estuaries and lagoons, where they mostly feed on aquatic invertebrates, amphibians, crabs, fish and worms (del Hoyo et al. 1992, Berruti 1997). Little is known about its breeding, but it is presumed to be monogamous and solitary breeder (Cyrus and Robson 1980). It has been reported that a normal clutch size (eggs per nest) is between three and four eggs and the sub-adults reach maturity and begin to breed at around three years of age (Clancey 1964). Naturally, they build large platform sticks nests with a central bowl lined with fine twigs and greenery on tall tree (Clancey 1964) predominantly close to water bodies (Cyrus and Robson 1980). The African woolly-necked stork was identified as a highly sensitive species that avoided human disturbance.

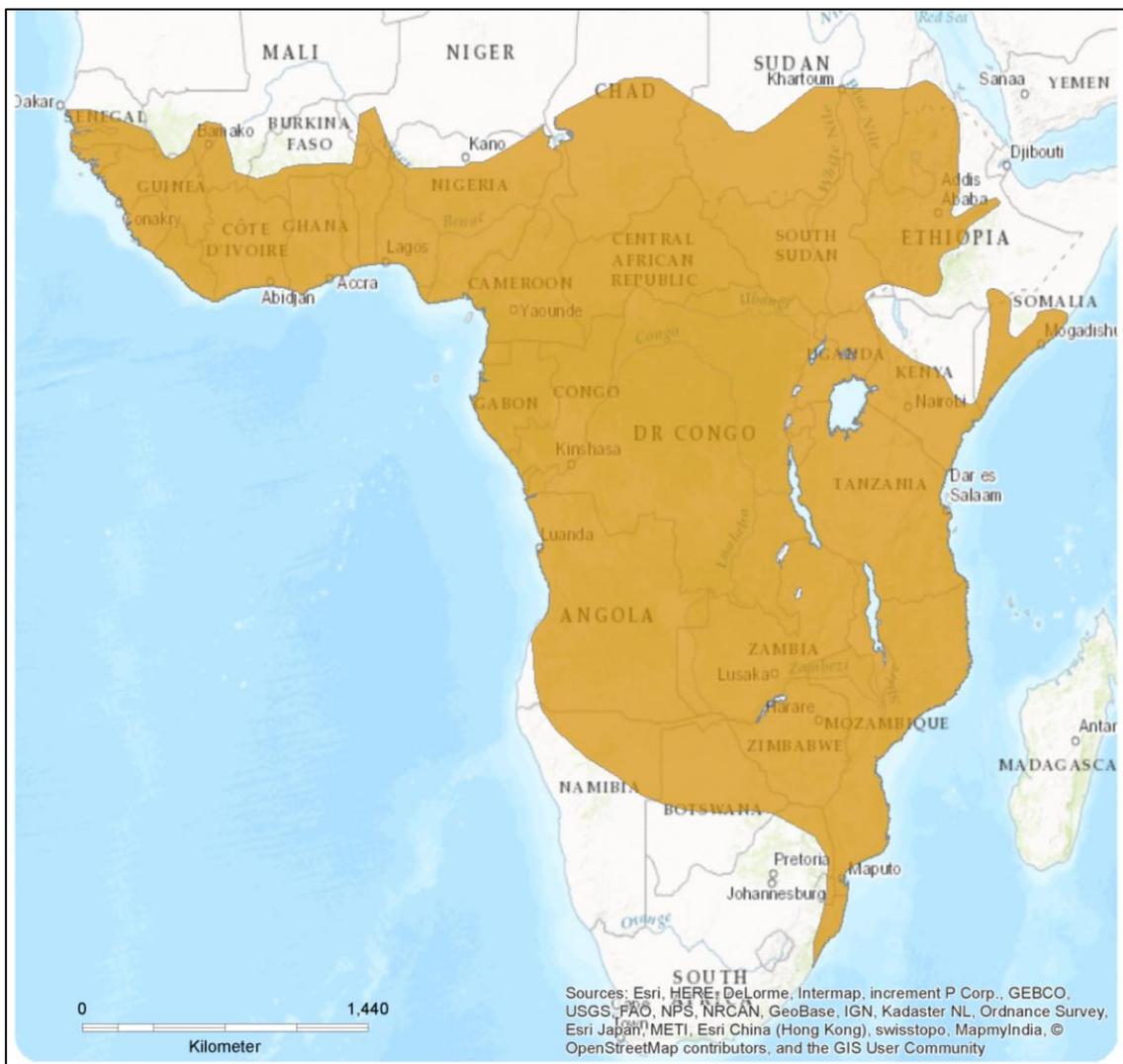


Fig. 1.1. Map showing the distribution of the African woolly-necked stork in Africa (Source: IUCN 2018).

1.5 Motivation

Typically, African woolly-necked storks are highly sensitive to human disturbance (Clancey 1964). In the 1980's, the African woolly-necked stork was considered as one of the rarest storks in South Africa (Clancey 1964, Cyrus and Robson 1980) thus listed in the Red Data List for Endangered Species (Brooke 1984). Recently, however, African woolly-necked storks have started colonising urban environments especially in KwaZulu-Natal, South Africa (Allan 2012, SABAP2 2018). African woolly-necked stork numbers have since increased considerably in KwaZulu-Natal leading to their delisting from endangered red list to least concern species in 2004 (Birdlife 2014, SABAP2 2018). The species has also expanded its range dramatically and is now commonly sighted further inland (SABAB2 2018) especially in suburban areas of KwaZulu-Natal. Furthermore, this species is now successfully breeding in suburban areas.

Despite the recovery and persistence of African woolly-necked storks in the urbanised environment of South Africa, no ecological research has been conducted on this species in the country. Consequently, this study examined several key aspects of the ecology of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa. Given the ongoing anthropogenic land-use change and the scarcity of data on urban birds in Africa, it is of high importance to understand how avian species persist and utilise resources in urbanised environments.

1.6 Aims and objectives

The on-going urbanisation and the ability of African woolly-necked storks to persist in urban environments suggest that base-line data on habitat selection of this species is important for suburban planning and management. The aim of this study was to understand aspects of urban ecology of the African woolly-necked storks in KwaZulu-Natal, South Africa. The objectives

of the study were 1) to determine long-term occupancy trends of African woolly-necked storks as a function of anthropogenic development in KwaZulu-Natal, 2) to investigate the extent (if any) to which householders in urban and suburban areas provide supplementary food to African woolly-necked storks, 3) to determine nest site selection and nesting habit of African woolly-necked storks, and 4) to document breeding behavior and nestling provision of the African woolly-necked storks over three breeding seasons in suburban areas of KwaZulu-Natal.

1.7 Thesis outline

This thesis consists of six chapters and four of the chapters (2 to 5) are presented as data chapters for publication in relevant peer reviewed journals. Thus, some repetitions in the chapters were unavoidable, particularly in relation to methods. The chapters are arranged in the following outline:

Chapter 2. Long-term trends (1992-2017) in occupancy, colonisation and decreased local extinction of African woolly-necked storks in KwaZulu-Natal, South Africa

Chapter 3. Citizen science reveals widespread supplementary feeding of African woolly-necked storks in suburban areas of KwaZulu-Natal South Africa

Chapter 4. Nest site selection of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa, and implications for its requirements

Chapter 5. Nestling provision and breeding behaviours of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa

Chapter 6. The concluding chapter that summarizes the various components of this study.

1.8 References

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CHAPTER 2

Long-term trends (1992-2017) in occupancy, colonisation and decreased local extinction of African woolly-necked storks in KwaZulu-Natal, South Africa

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2.1 Abstract

Understanding how the presence of species is affected by landscape modification is crucial for the conservation of biodiversity. In this study, we used data from a citizen science monitoring program, the Coordinated Waterbird Counts, to determine long-term trends (1992 - 2017) in occupancy, colonisation and extinction of African woolly-necked storks (*Ciconia microscelis*) as a function of change in land cover across KwaZulu-Natal Province, South Africa. We analysed data using dynamic occupancy models. African woolly-necked stork wetland occupancy was relatively stable ($\psi = 0.37-0.39$) across years, suggesting that extinction was balanced by recolonisation. Seasonal shortages of food resources associated with the dry season might account for the lower detection probability in winter. Although occupancy was stable, African woolly-necked stork populations rapidly extended their distribution range to urbanised environments over the duration of monitoring, becoming common in KwaZulu-Natal. Interestingly, changes in land cover decreased the probability of wetland occupancy. However, the increased area of anthropogenic development increased the probability of colonisation and decreased the probability of extinction. African woolly-necked stork populations have taken advantage of recent anthropogenic development especially man-made wetlands and anthropogenic supplementary food. Our results contradict the traditional view that only natural wetlands far away from human disturbance support high colonisation of this bird species. Our results indicated that African woolly-necked storks, once rare and endangered throughout the region, now have a stable population in KwaZulu-Natal. This study showed the power of long-term citizen science data to assess factors that influence occupancy trends in waterbird populations.

Keywords: anthropogenic development, citizen science, dynamic occupancy model, storks, wetland, colonisation, extinction.

2.2 Introduction

Land-use change is the greatest threat to terrestrial biodiversity and ecosystem services worldwide (Cohen 2006, Aronson et al. 2014, Seress and Liker 2015). Of the ecosystems influenced by land-use change, natural wetlands appear particularly sensitive and vulnerable (Dudgeon et al. 2004, Matchett and Fleskes 2017). Wetland loss and degradation has been extensive across the world (Kentula et al. 2004; Valente et al. 2011, Lee et al. 2006, Li et al. 2014, Kleijn et al. 2014, Glisson et al. 2017, Matchett and Fleskes 2017, Jia et al. 2018) and South Africa is no exception where over 50% of natural wetlands have been lost (Harebottle 2012, Dini and Everard 2016). South Africa's wetlands are one of the most threatened ecosystems in the country primarily because of rapid growth of human populations, agriculture and urban sprawl (Hiestermann and Rivers-Moore 2015, Herbst 2015, Dini and Everard 2016).

With the loss of natural wetlands, artificial wetlands are becoming increasingly important as habitats (breeding and foraging) for waterbirds (Breininger and Smith 1990, Murray et al. 2013). Some waterbird species have expanded their range over the past decades for this reason, thereby increasing colonisation rates to new sites previously not occupied (Macdonald et al. 1986, Treinys et al. 2008, Martin et al. 2010, Duckworth and Altwegg, 2014, Singh and Downs 2016). For example, hadeda ibis (*Bostrychia hagedash*) benefited from human-made wetlands and are now thriving across South Africa (Duckworth and Altwegg 2014, Singh and Downs 2016). Hockey et al. (2011), identified the ability of waterbird species to use man-made wetland habitats as an important factor contributing to their range expansion.

Some waterbird species have recovered from endangered or near extinction status (Hockey et al. 2011, Scholte 2006). For instance, creation and rehabilitation of floodplains resulted in the recovery of *Ciconiiformes* in Cameroon (Scholte 2006). In South Africa, one species that has recovered from endangerment and is now more common, is the African woolly-necked stork (*Ciconia microscelis*). Despite considerable changes in African woolly-necked

stork numbers and occupation of sites, no studies have been conducted on the occupancy trends of this species in South Africa. We therefore, applied dynamic occupancy models using long-term (1992-2017) presence/absence data from Coordinated Waterbird Counts (CWAC) citizen science surveys in South Africa to assess African woolly-necked stork occupancy. The aim of this study was to determine trends in long-term wetland occupancy, colonisation and extinction of African woolly-necked storks as a function of anthropogenic development and area of wetlands in 70 wetlands in KwaZulu-Natal Province, South Africa. We also explored whether estimates of extinction, colonisation, detection and occupancy varied among wetland types (i.e. among river, man-made dams, estuaries and wastewater treatment plants) and status (protected or unprotected). We predicted that occupancy would be positively associated with natural wetlands (e.g. rivers) and negatively associated with man-made wetlands (e.g. wastewater treatment plants).

As the African woolly-necked stork has recovered from being endangered in South Africa (del Hoyo et al. 2018), we predicted that the occupancy trend will significantly increase between 1992 and 2017. Since the African woolly-necked stork is now common and widespread in KwaZulu-Natal especially in suburban areas (SABAP 2018, Thabethe and Downs 2018), we predicted that occupancy of African woolly-necked storks would be positively associated with changes in land cover. We also predicted that occupancy and colonisation will be positively associated with wetland areas. Our study serves as an example of the analysis of long-term citizen science dataset using advance dynamic model occupancy methods that account for imperfect detection.

2.3 Methods

Study species

The African woolly-necked stork, indigenous to sub-Saharan Africa (Cyrus and Robson 1980), was recently confirmed to be a separate species from the Asian woolly-neck stork (*C. episcopus*) (del Hoyo et al. 2018). It is distributed across tropical Africa with a separate population in sub-Saharan Africa (del Hoyo et al. 2018). In South Africa, the African woolly-neck stork was previously listed in the Red Data List for Endangered Species but has since been reclassified twice and is now listed as Least Concern due to increasing population numbers (Clancey 1964, Cyrus and Robson 1980, BirdLife International 2018). The species seem to have expanded range southwards along the coast (Allan 2012, SABAP 2018). Evidence suggests that the urban population of the African woolly-necked stork are residential throughout the year although there are claims that the species used to be migratory (Clancey 1964, del Hoyo et al. 2018, Thabethe and Downs 2018). Naturally, the African woolly-necked stork is highly dependent on wetlands with tall trees for feeding and breeding (Clancey 1964). It feeds on amphibians, insects, small mammals and reptiles along water bodies and nest solitary on tall trees overhanging wetlands (Clancey 1964, Cyrus and Robson 1980). African woolly-necked stork occurs around natural wetlands such as rivers, and lagoons (Clancey 1964, Cyrus and Robson 1980). With increasing wetland degradation in South Africa, it is of urgent importance to understand specific ecological requirements such as occurrence, distribution and wetland preference of the recovering waterbird species such as the African woolly-necked stork.

Study area

KwaZulu-Natal Province is in the eastern part of South Africa (Fig. 2.1). Wetlands are well presented in this province covering approximately 5% of the province (4200 km²) partly

because of varied geology, topography and climate (Hiestermann and Rivers-Moore 2015). KwaZulu-Natal has an array of diverse natural resources that makes it suitable for varied agricultural production, variety of industrial and increased urban areas (Fig. 2.1). These activities are increasingly causing pressure on the province's natural resources including wetlands (Hiestermann and Rivers-Moore 2015).

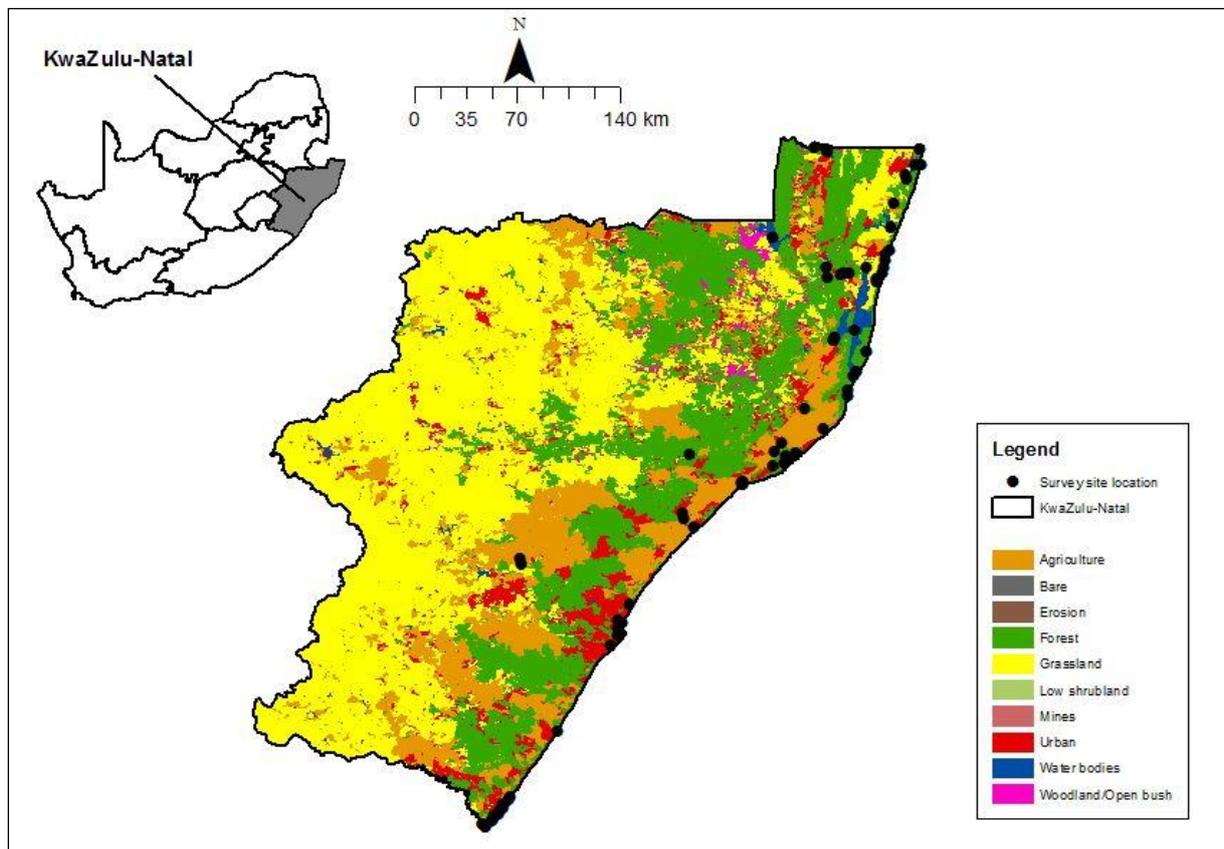


Fig. 2.1: Location of surveyed 70 CWAC wetland sites (black dots) used in this study across KwaZulu-Natal Province, South Africa.

Coordinated Waterbird Counts (CWAC)

We utilised 26 years (1992-2017) of the CWAC site-based data to determine trends in occupancy of the African woolly-necked storks in KwaZulu-Natal, South Africa. The CWAC

project is a large citizen science of waterbird lists collected by both professional and amateur volunteers (Harrison et al. 2008). The CWAC project was launched in 1992 with the aim of monitoring populations of waterbirds by conducting regular summer and winter counts at South Africa's major wetlands (including: pans, rivers, man-made dams, lakes, vleis, estuaries, lagoons and wastewater treatment plants) (Harrison et al. 2008). Generally, CWAC counts take place twice a year where summer counts are conducted between the 15 of January to the 15 February, while winter counts are conducted in July. These months represent summer and winter seasons and it was considered appropriate to conduct surveys at these times to account for seasonal variability of the species. Apart from these regular counts, the public is encouraged to conduct as many counts as they can where possible. For each survey, programme participants spend a minimum time of 2 h of intensive birding, recording all waterbirds species seen within the particular wetland. Survey techniques are consistent from year to year and standard protocols are followed by project participants. Protocols include the number of counts conducted per site, time of the day, routes followed, viewing aid (e.g. binoculars) and counting techniques. Counters are encouraged to be experienced in identifying waterbirds and trainings are provided to interested volunteers if necessary. All the information regarding the CWAC project, guidelines for the completion of the census form and protocols are readily available on the CWAC website (<http://cwac.adu.org.za/forms.php>). CWAC data are available over extensive geographic areas and time and therefore suitable for population trend of waterbirds studies. Due to logistic constraints and nature of the project, surveys within years were not conducted simultaneously across sites. Counts were done at the same points/sites over several years. For our analyses, we collapsed these counts down to whether the African woolly-necked stork was detected or undetected in each count.

Wetlands used in CWAC are any water body which supports 500 or more individual waterbirds irrespective of the number of species (Harrison et al. 2008). The CWAC wetlands

that were used for analyses in this study were within the African woolly-necked stork range in the region of KwaZulu-Natal. In total, 70 wetlands were included in our study (Fig. 2.1).

Analytical design

To develop dynamic occupancy models, we used African woolly-necked stork data collated via the public based data (CWAC) between 1992 and 2017 and five site-covariates including wetland type, wetland status, area of anthropogenic development (agriculture and urbanisation), area of wetland, change in anthropogenic development and water bodies over 26 years. Observation of the African woolly-necked storks within a surveying period at a sampling site was taken as 1 (detection). Non-detection data were extracted from the CWAC data and consisted of all visits made without any recorded sightings of the African woolly-necked storks. The detection history of each site was summarised as binary presence data for each year for each site. We developed detection histories of 70 wetlands for African woolly-necked storks across 26 years (1992-2017).

Landscape covariates

We developed site specific covariates for use in analytical models of occupancy (Table 2.1). As global positioning systems (GPS) data for each surveyed wetland were available from CWAC website, we extracted the area of wetland and anthropogenic development (agriculture, exotic tree plantation and urban area) within 1 km buffer using ArcGIS 10.1 (ESRI, 2012) (ESRI, 2012, Redlands, CA, USA). South Africa's land cover for 2014 (originally with 72 classes) and 1990 (originally with 47 classes) were reclassified into 4 broad classes (wetlands, agriculture, exotic tree plantations, and urban area) to measure the land cover change between two-time periods (2014 and 1990). We calculated the proportion of area in a site covered by comparing each reclassified land cover using the National Land Cover layers for 1990 and

2014 (Van den Berg et al. 2008). We compared whether there was habitat modification (particularly gain in anthropogenic development) between 1990 and 2014 within 1 km buffer of the survey point. A score of 1 was given if there was a change and score of 0 was given if there was no change in land cover. Continuous covariates such as the area of anthropogenic development and the area of wetlands were standardised to a z-score. These covariates were standardised to ensure that each covariate had equal predictive power thus ensuring that values were not skewed by unevenly large values. Recently, Zheng et al. (2015) found that waterbirds richness and abundance increased more rapidly in protected wetlands than in unprotected wetlands in China. We therefore tested the efficiency of conservation actions and analysed whether the recent increase in African woolly-necked storks' population was more in protected wetlands compared with unprotected wetlands. Sundar (2006) revealed that four waterbird species including Asian woolly-necked stork (*Ciconia episcopus*) preferred natural wetlands over flooded agriculture fields. Consequently, we used wetland type as a predictor covariate to determine whether there was any preference of certain wetland type. All covariates were chosen because of their hypothesised influence on African woolly-necked storks.

Table 2.1. Site and landscape characteristics measured at 70 wetlands sites surveyed for African woolly-necked storks in KwaZulu-Natal, South Africa

Code	Covariate	Description
Land cover change	Change (1), No change (0)	Calculated as a percentage of change (gain) or no change (stay the same) in land cover between 1992 and 2017
Anthropogenic development	Percentage of development within 1 km radius	Calculated as the area of Development/size of the buffer
Area of wetland	Percentage of wetland within 1km radius	Calculated as the areas of wetland/size of the buffer
wetlandtypepe	type of wetland	Estuary, lake, pan, river, man-made dam, wastewater treatment plants
wetstatus	wetland status (protected (1) or non-protected (0))	protected by Ezemvelo KZN or not protected

Data analyses

We used dynamic season (also called multi-season) modelling approach of McKenzie et al. (2003) to model trends in African woolly-necked stork occupancy between 1992 and 2017. Dynamic model allows the quantification of species occupancy while correcting for imperfect species detectability based on repeated sampling in time and space (McKenzie et al. 2003). We performed dynamic occupancy models using the function “*colext*” in the package *unmarked* (Fiske and Chandler 2011) in program R 3.1 (R Core Team 2013). The stepwise procedure was then used to select a list of supported models. Firstly, we independently assessed detection probability (p) by fitting various covariates for the detection parameter and the most important detection model structure was based on the Akaike information criterion (AIC). The best detection model structure was then used to estimate occupancy (ψ), colonisation probability (γ) and extinction probability (ε). We allowed potential covariates for (ψ) (γ) (ε) and (p) to vary individually or in combination. We used investigated year as a categorical variable for detection. Results indicated that detection did not vary among years. Therefore, year was not considered further as a covariate.

In the dynamic occupancy model, annual occupancy models are derived from colonisation and extinction probabilities where colonisation is the probability that a site unoccupied by African woolly-necked storks in year t would be occupied in year $t+1$ while extinction is the probability that a site occupied by African woolly-necked storks in year t is unoccupied in year $t+1$. Occupancy is the probability that the African woolly-necked stork occurs in the site during 1st year of the survey and detection (p) is the probability to detect at least one African woolly-necked stork each year. The model selection was based on AIC (Burnham and Anderson 2002), where the smaller AIC value indicated the best model. Models with a delta AIC of less than two were deemed competitive (Burnham and Anderson 2002).

We drew conclusions about strengths of evidence of relationships between covariates ψ , γ , ε and p based on 95% confidence intervals of coefficients of the direction of relationships. We considered confidence intervals not containing zero to indicate the strongest relationships, while confidence intervals centred on zero were considered to indicate little or no evidence of relationships.

2.4 Results

Probability of detecting African woolly-necked stork and abundance

During 26 years of surveys, African woolly-necked storks were detected on 48 of 70 (naïve wetland detection rate = 69%) wetlands visited. They were detected in more than one year at 48 of the 70 (69%) wetlands. The number of wetlands at which African woolly-necked storks were detected fluctuated from 4 to 24 between 1992 and 2017. The African woolly-necked stork individual numbers per year fluctuated between 1992 and 2017 (Fig. 2.2). The minimum number of individuals observed in a year was 37 in 1992 while the maximum was 352 in 2002 (Fig. 2.2). Number of occupied wetland sites increased from 2 to 19 over the study period (Fig. 2.3). Estuaries were the first two wetlands to be occupied in 1992. Our findings showed that detection probability was not perfect, nor was it constant over space and time. The detection probability as a function of season (winter and summer) within year had a strongest support and was used in the subsequent analysis of occupancy. Detection probability was lower (0.4) during the winter surveys (July) within each year while higher (0.6) during summer (January - February) surveys. The seasonal difference in probability of detection is possible due to expected annual variation in precipitation and temperature. Year did not influence the probability of detecting African woolly-necked storks, however it fluctuated between 1992 and 2017 (Fig. 2.4a).

Occupancy

Our results suggest that the African woolly-necked stork occupancy was not constant among study wetland sites. The wetland occupancy trend was relatively stable ($\psi = 0.37-0.39$) throughout the study period (Fig. 2.4b). There were five best-approximating models with delta AIC < 2; the model with the most support had a model weight (w) of 0.11 (Table 2.2). The best supported model indicated that the occupancy of African woolly-necked storks was driven by land cover change (Tables 2.2 and 2.3). Occupancy probability was higher (0.59) in wetlands that had not had land cover change and lower (0.29) where land cover had changed (Fig. 2.4c). Although the correlation was weak, African woolly-necked stork occupancy increased with area of wetland (Fig. 2.4d).

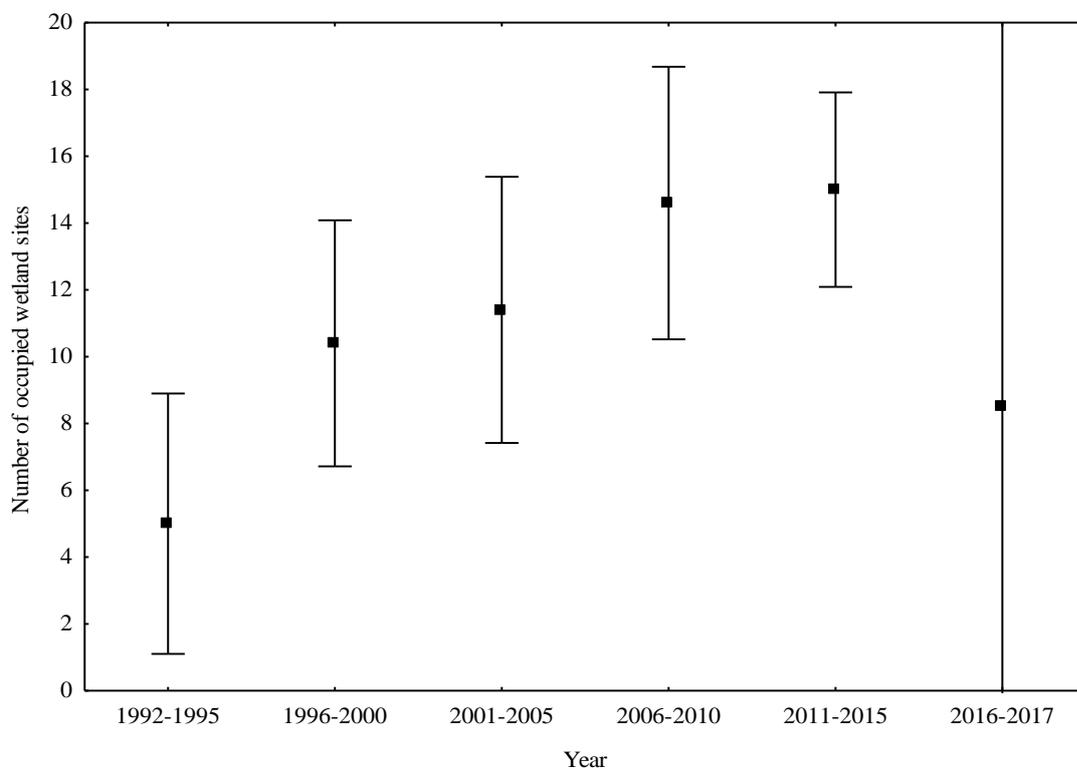


Fig. 2.2: Mean number of wetlands occupied by African woolly-necked storks in KwaZulu-Natal between 1992 and 2017.

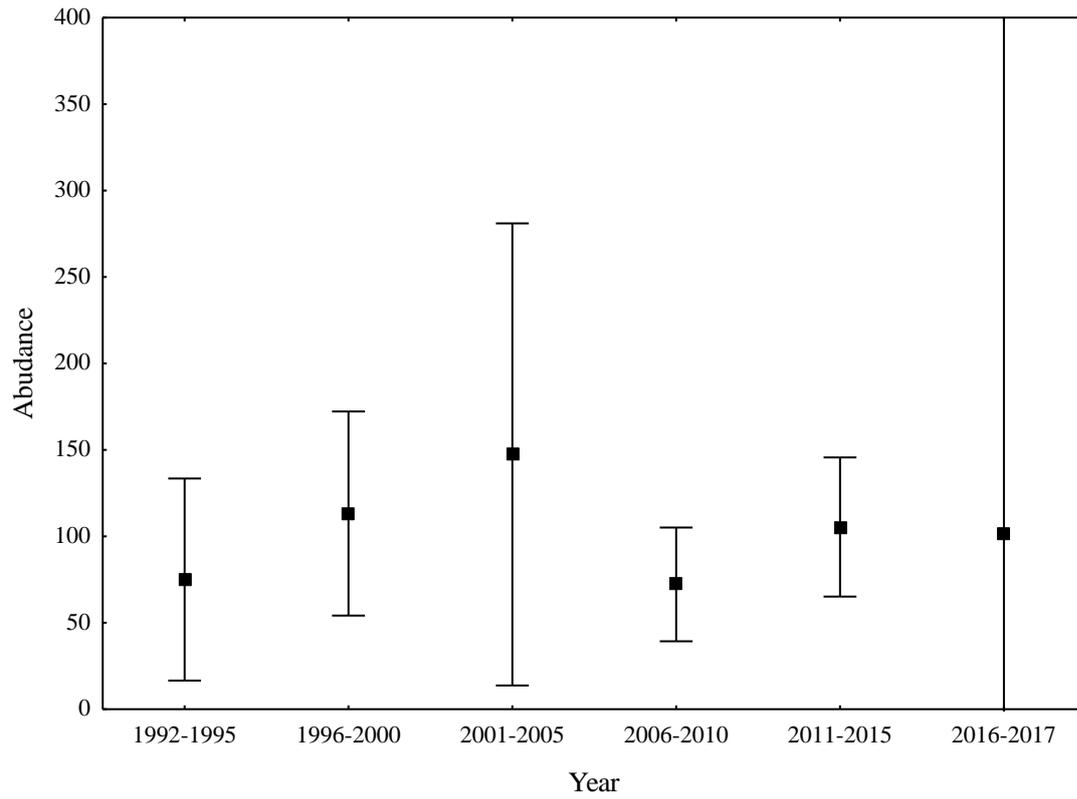


Fig. 2.3. Abundance of African woolly-necked stork between 1992 and 2017 in KwaZulu-Natal

Table 2.2. Dynamic occupancy models to estimate probability of African woolly-necked stork occupancy (ψ), probability of colonisation (γ), probability of extinction (ε) and probability of detecting (p). Model selection is based on Akaike's information criterion. Delta AIC (ΔAICc) is the difference in AIC values between each model with the low (best) model, w_i is the AIC model weight, K is the number of parameters in the models. Models in bold are best models.

Model	K	AICc	ΔAICc	w
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type+wetland-area+developed-area})p(\text{season})$	12	1649.64	0	0.1908
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type+wetland-area+developed-area})p(\text{season})$	13	1651.46	1.82	0.0766
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type+wetland-area+developed-area+landscape-change})p(\text{season})$	13	1651.52	1.88	0.07461
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type})p(\text{season})$	10	1651.59	1.95	0.07195
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type+wetland-area+developed-area})p(\text{season})$	13	1651.61	1.97	0.07112
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type+wetland-area})p(\text{season})$	11	1652.01	2.37	0.05837

$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type+developed-area})p(\text{season})$	11	1652.51	2.87	0.04548
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type+wetland-area})p(\text{season})$	12	1652.53	2.89	0.04491
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type+wetland-area+landscape-change})p(\text{season})$	12	1652.58	2.95	0.04373
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type})p(\text{season})$	11	1652.82	3.18	0.03889
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type})p(\text{season})$	11	1653.27	3.63	0.03102
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type+wetland-area+developed-area+landscape-change})p(\text{season})$	14	1653.37	3.74	0.02948
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type+wetland-area+developed-area})p(\text{season})$	14	1653.43	3.79	0.02867
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type+landscape-change})p(\text{season})$	11	1653.45	3.81	0.02841
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type+wetland-area+developed-area+landscape-change})p(\text{season})$	14	1653.5	3.86	0.0277

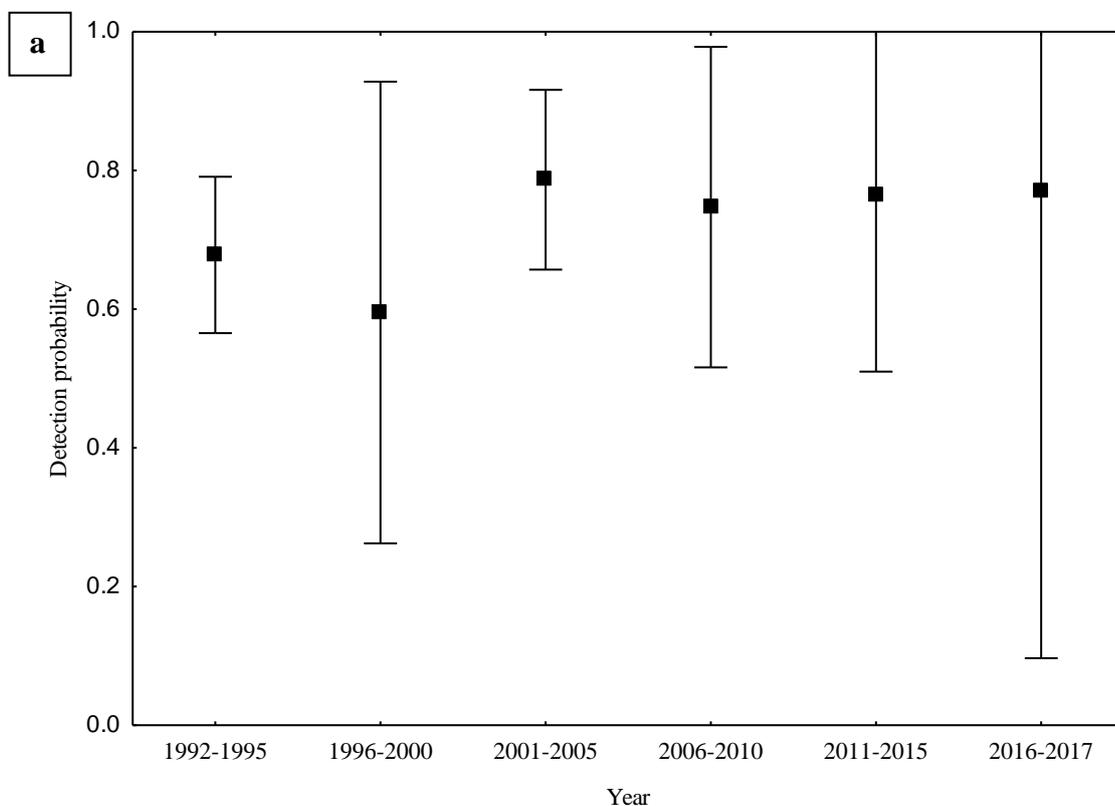
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type+wetland-area+landscape-change})p(\text{season})$	13	1653.73	4.09	0.02467
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-type+wetland-area})p(\text{season})$	12	1653.98	4.34	0.02175
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type+developed-area})p(\text{season})$	12	1654.31	4.67	0.01845
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type})p(\text{season})$	12	1654.47	4.83	0.01707
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type+wetland-area})p(\text{season})$	13	1654.53	4.89	0.01653
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type+landscape-change})p(\text{season})$	12	1654.81	5.18	0.01435
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-type+wetland-area+developed-area+landscape-change})p(\text{season})$	15	1655.35	5.71	0.01098
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-area+developed-area})p(\text{season})$	11	1658.9	9.26	0.00186
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{developed-area})p(\text{season})$	10	1659.48	9.84	0.00139

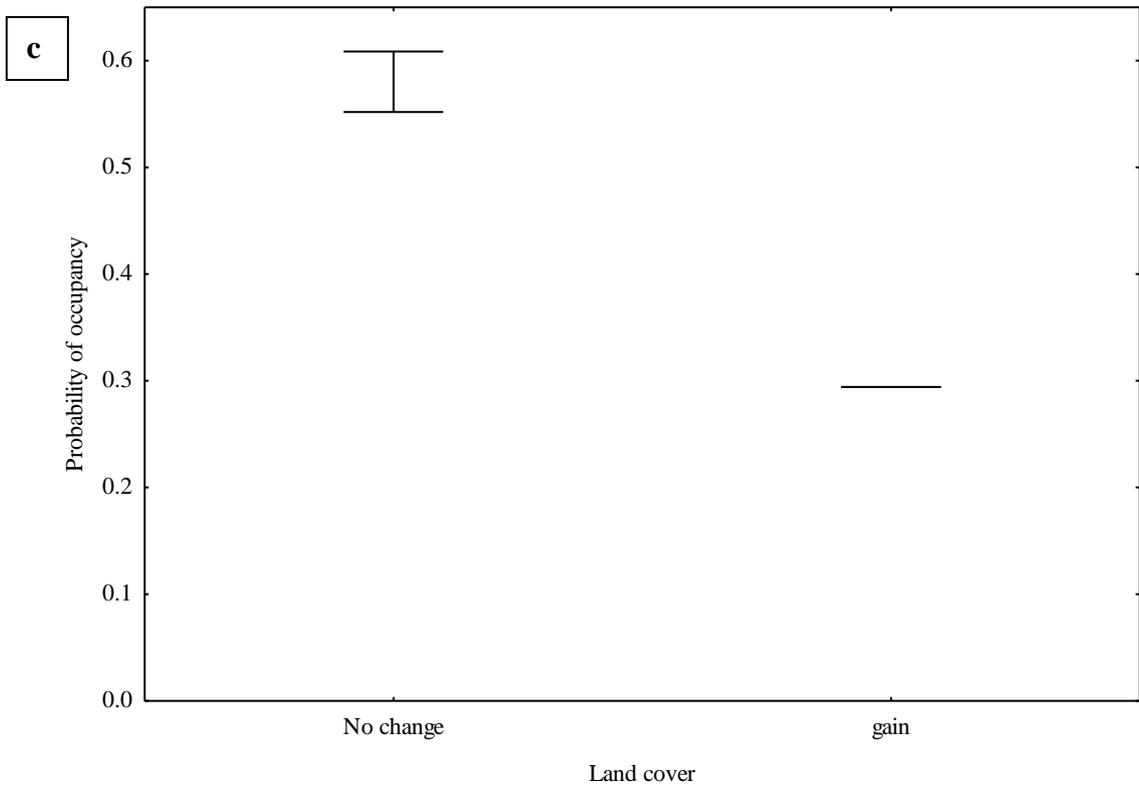
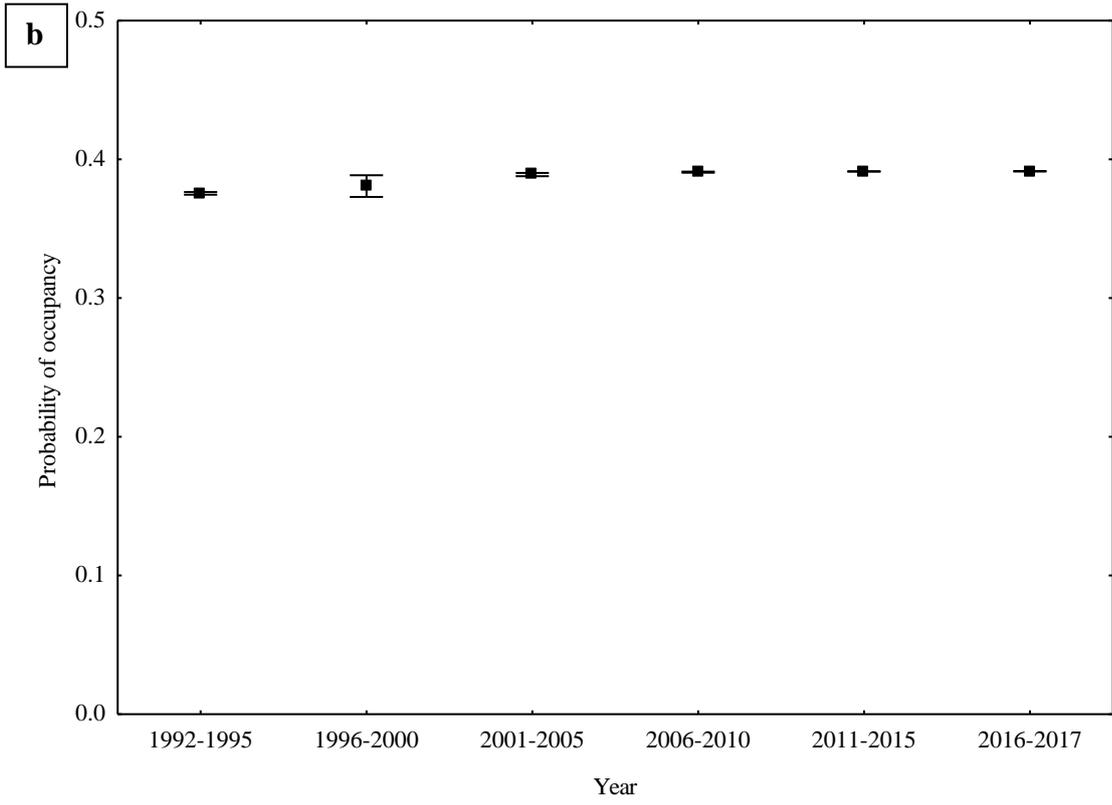
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status})p(\text{season})$	10	1659.92	10.29	0.00111
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-area})p(\text{season})$	10	1660.13	10.49	0.00101
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{landscape-change})p(\text{season})$	10	1660.29	10.65	0.00093
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-area+landscape-change})p(\text{season})$	11	1660.39	10.76	0.00088
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(.)p(\text{season})$	10	1660.39	10.76	0.00088
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-area+developed-area+landscape-change})p(\text{season})$	12	1660.5	10.87	0.00083
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-area+developed-area})p(\text{season})$	12	1660.89	11.25	0.00069
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+wetland-area})p(\text{season})$	11	1660.91	11.28	0.00068
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{developed-area})p(\text{season})$	11	1660.96	11.32	0.00066
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+developed-area})p(\text{season})$	11	1661.3	11.66	0.00056
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{developed-area+landscape-change})p(\text{season})$	11	1661.46	11.83	0.00052

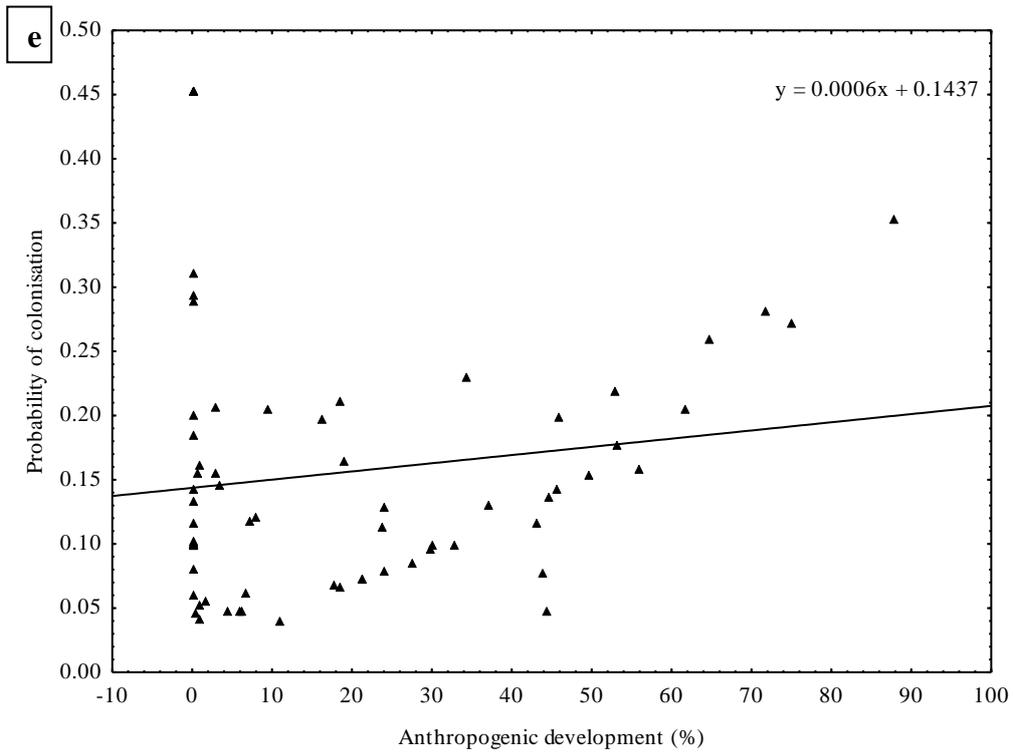
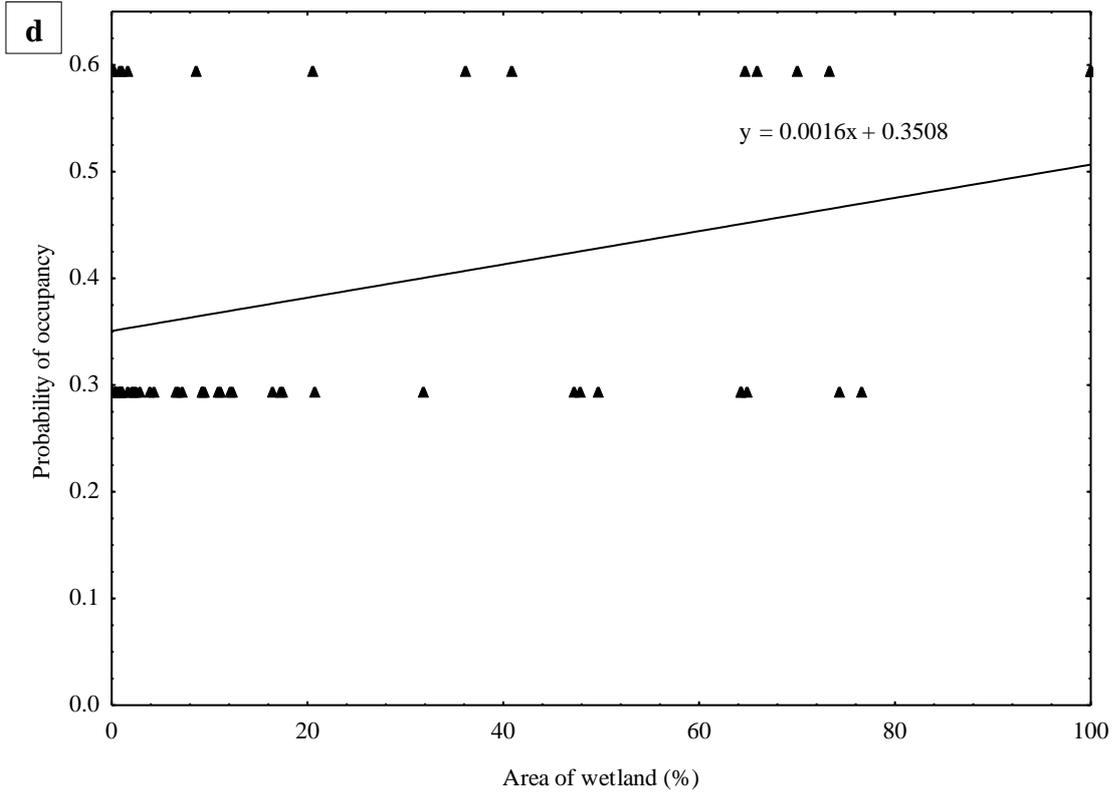
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status})p(\text{season})$	11	1661.51	11.87	0.00051
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{landscape-change})p(\text{season})$	11	1661.68	12.04	0.00046
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-status+landscape-change})p(\text{season})$	11	1661.8	12.16	0.00044
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-area})p(\text{season})$	11	1662.03	12.4	0.00039
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{wetland-area+developed-area+landscape-change})p(\text{season})$	13	1662.48	12.84	0.00031
$\psi(\text{landscape-change})\gamma(\text{wetland-area+developed-area+landscape-change})\varepsilon(\text{developed-area+landscape-change})p(\text{season})$	12	1662.94	13.3	0.00025

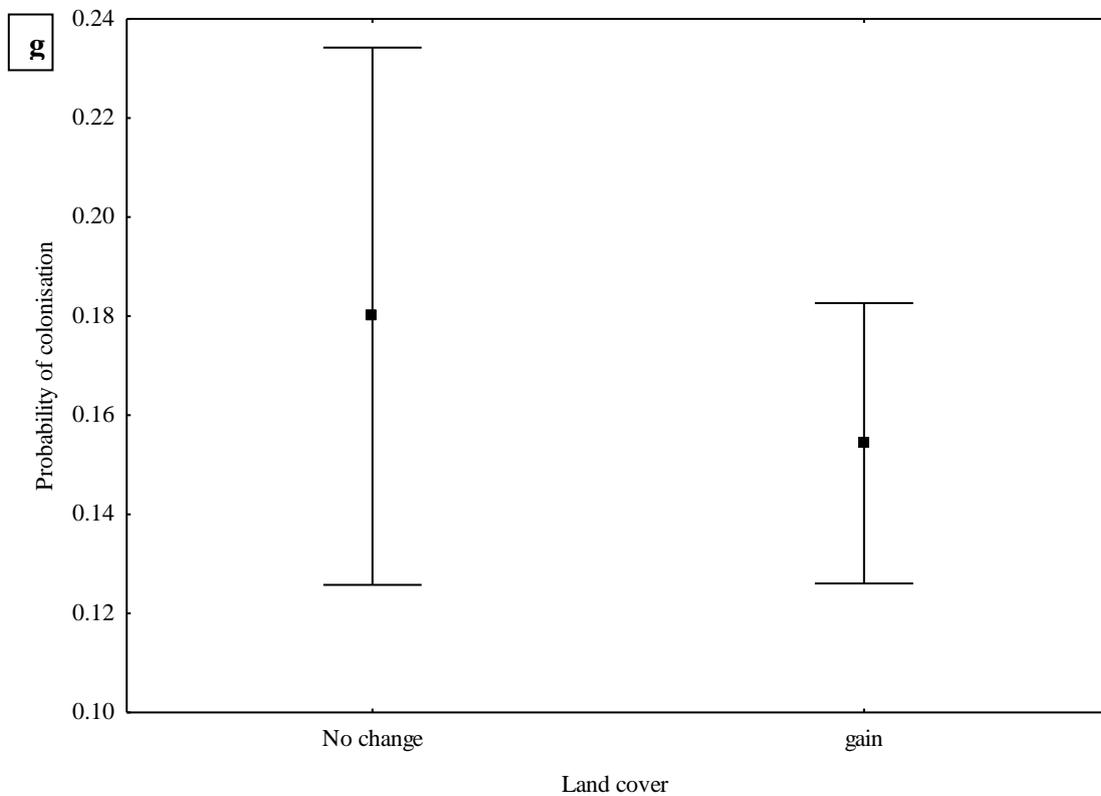
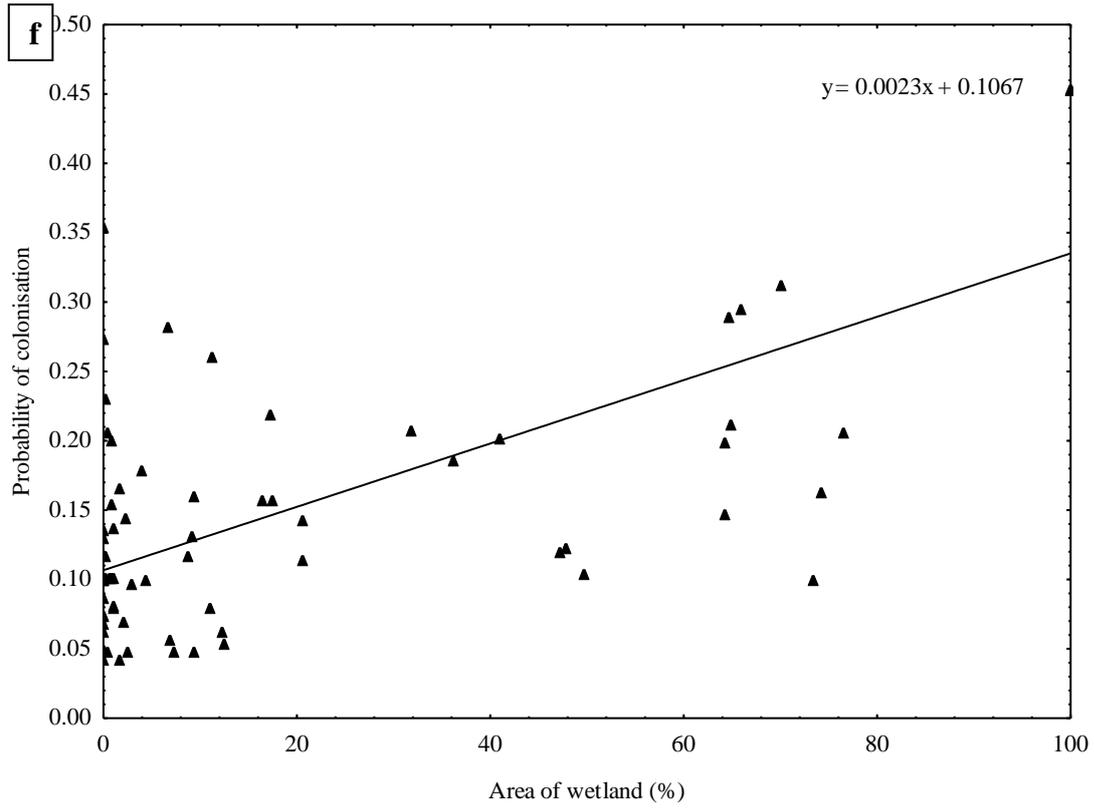
Colonisation and extinction probability of African woolly-necked storks

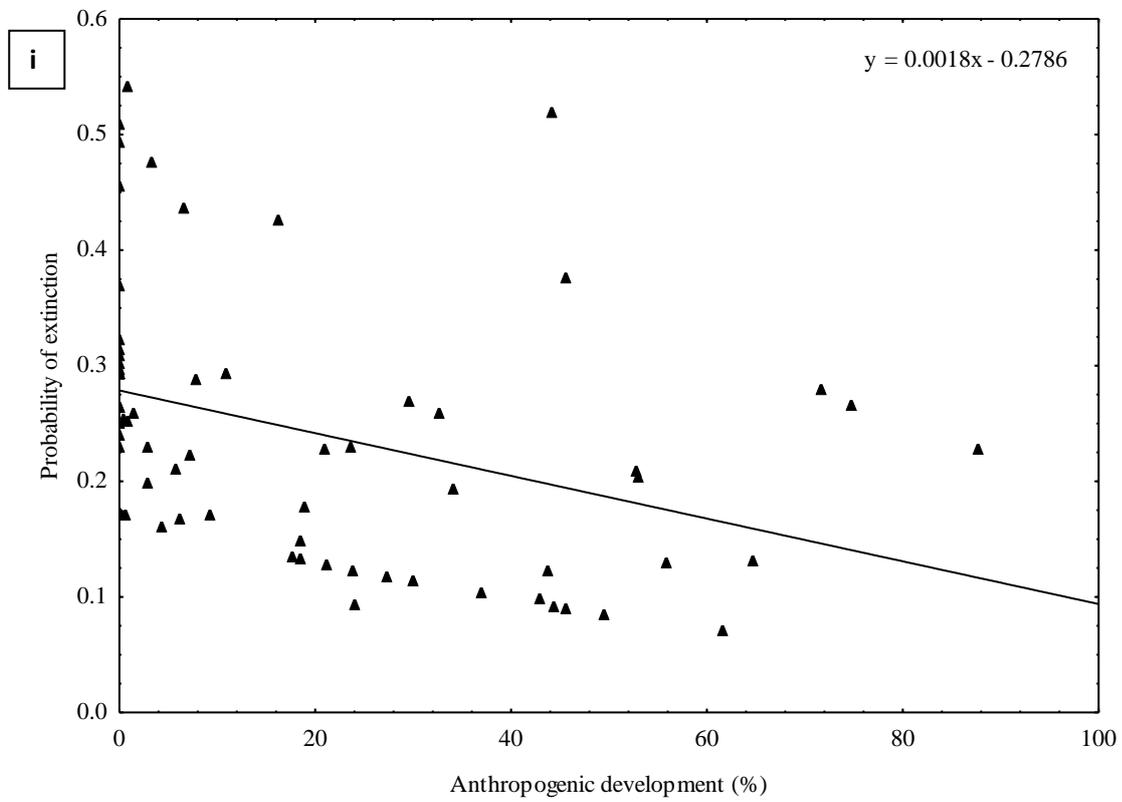
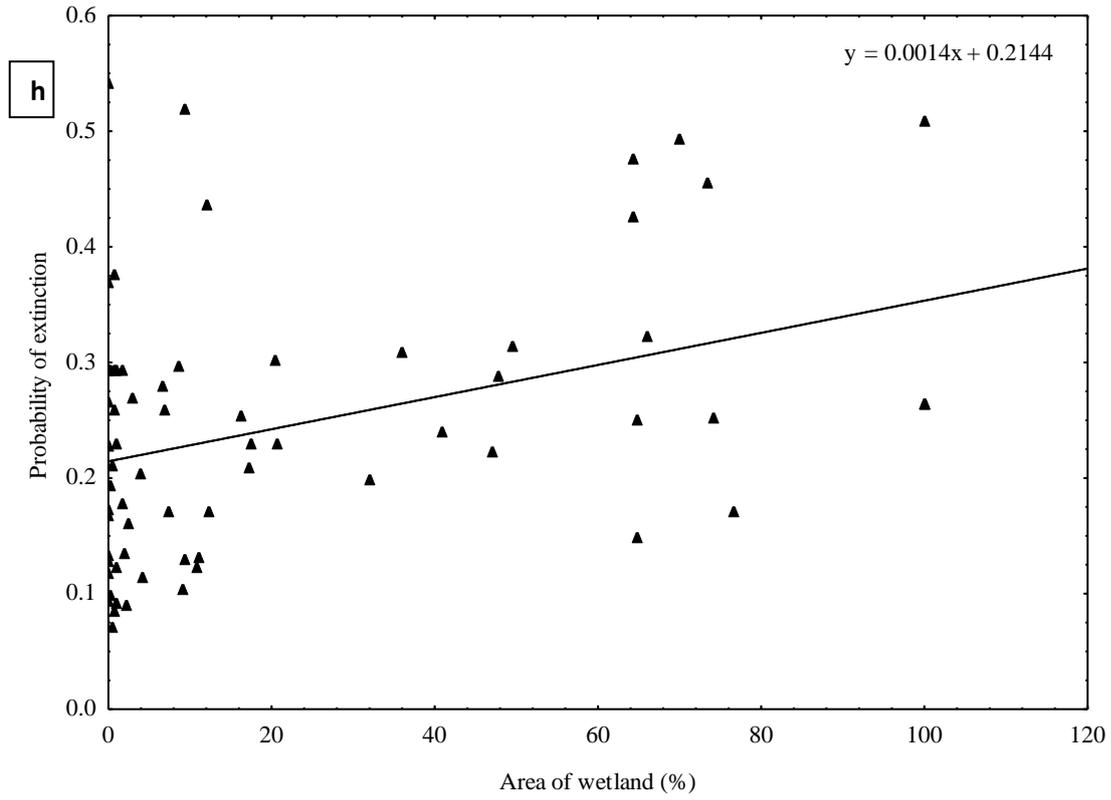
The best supported models indicated that the colonisation of African woolly-necked storks was driven by land cover changes, area of anthropogenic development and area of wetland (Table 2.2) while local extinction was driven by wetland type, areas of water and area of anthropogenic development (Table 2.2). The probability of colonisation was positively affected by the area of wetland (Fig. 2.4e) and area of anthropogenic development (Fig. 2.4f). Change in land cover decreased probability of colonisation (Fig. 2.4g). Hence, the probability of colonisation increased with area of both wetland and development (Fig. 2.4e and 2.f). The probability of extinction increased with increasing areas of wetland (Fig. 2.4h) and decreased with area of anthropogenic development (Fig. 2.4i). The probability of extinction was highest in man-made dams followed by wastewater treatment plants, and at the lowest in estuaries (Fig. 2.4j).











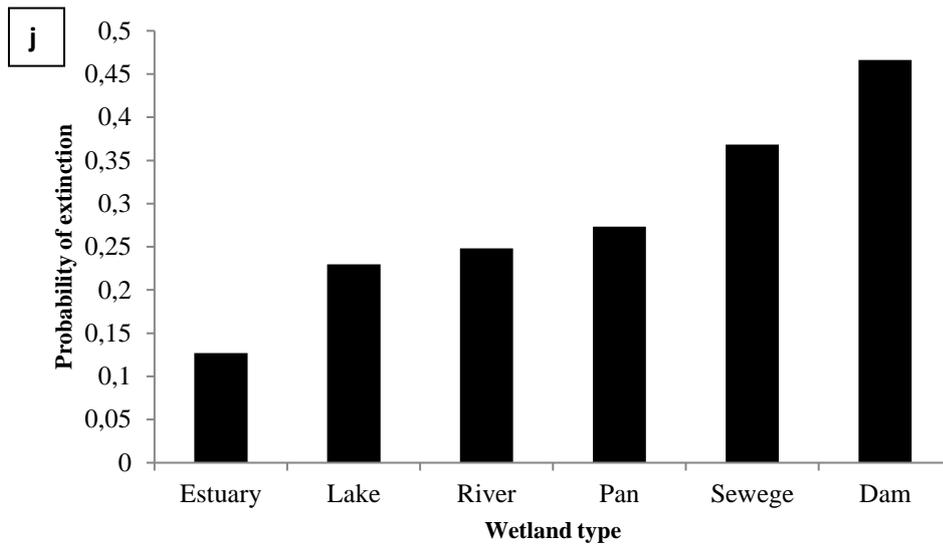


Fig. 2.4. Estimated relationships between parameters and covariates from top dynamic occupancy models for African woolly-necked storks where (a) mean probability of detection of African woolly-necked storks across 26 years (1992-2017), (b) estimated mean probability of occupancy across 26 years, (c) estimated mean probability of occupancy related to land cover change (d) estimated mean probability of occupancy related area of areas of wetland (e) estimated mean probability of colonisation related to area of anthropogenic development (f) estimated mean probability of colonisation related to area of wetland (g) estimated mean probability of occupancy related to land cover change (h) estimated mean probability of extinction related to area of anthropogenic development (i) estimated mean probability of extinction related to related to area of wetlands, and (j) estimated mean probability of extinction related to wetland type.

Table 2.3. Model average parameter estimates, standard errors (SE), and 95% confidence intervals (CIs) shown for each covariate from the top dynamic occupancy models.

Parameter	Covariate	Estimate	SE	LCI	UCI
ψ	Intercept	1.33	1.34	0.99	0.32
	Landscape-change	-2.26	1.58	-1.43	0.15
γ	Intercept	-1.30	0.28	-4.65	6.5E-06
	Wetland-area	-0.74	1.06	-1.69	0.15
	Developed-area	-0.74	1.06	-1.69	0.15
	Landscape-change	-0.74	1.06	-1.69	0.15
ε	Intercept	-1.41	0.28	-4.96	7.01E-07
	Wetland-area	-0.40	0.18	-2.17	0.02
	Developed-area	-0.85	0.51	-2.92	0.06
	Wetland-type	0.39	0.12	3.24	0.001
	Wetland status	0.19	0.48	0.40	6.84E-01
p	Intercept	0.22	0.14	1.51	0.12
	season	-0.44	0.14	-3.08	0.002

2.5 Discussion

To the best of our knowledge, this study is the first to investigate wetland occupancy trends of African woolly-necked storks in South Africa. Overall, our results showed that wetland occupancy of African woolly-necked stork in KwaZulu-Natal, South Africa, remained stable over time. The number of individuals occupying studied wetlands fluctuated over time. This was interesting and unexpected since the African woolly-necked stork population has rapidly increased in South Africa so much so that it was removed from endangered species list to Least Concern species (del Hoyo et al. 2018). Although occupancy was stable, African woolly-necked stork populations rapidly extended their distribution range to cities from 1992 to 2017, becoming widespread in man-made wetlands. Consistent with our findings, a recent study

revealed that African woolly-necked storks are widespread and common in urban and suburban areas of KwaZulu-Natal where they benefit from direct supplementary feeding in domestic gardens and forage in urban parks and recreation areas (Thabethe and Downs 2018). This species also successfully nests in suburban areas due to the planting of ornamental trees in suburban areas and to their growing offering of suitable nesting sites with tall enough trees such as *Eucalyptus* spp. and *Pinus* spp. (SABAP2 2018, Thabethe and Downs 2018 unpublished data). The African woolly-necked stork is not the first avian species whose species recovery is associated with their occurrence in urban areas (Francois et al. 2008). Copper's hawks (*Accipiter cooperii*) are now widespread in urban areas of the United States of America and Canada following their recovery (Mannan and Boal 2008, Stout and Rosenfield 2010). Similar to our findings, Mannan et al. (2008) found evidence that urban areas provided high quality habitat for Copper's hawk, including high nesting density and food resources. There are several storks that are also associated with urban areas throughout the world, for instance, white storks (*Ciconia ciconia*) in Europe (Gilbert et al. 2016, Kopij 2017), marabou storks (*Leptoptilos crumeniferus*) in Africa (Pomeroy and Kibuule 2017), and wood storks (*Mycteria americana*) in the United States (Traut and Hostetler 2003). Interestingly, white storks in Poland are strictly associated with human settlements, where more than 99% of their nests are in settlements (Kopij 2017). In addition, creation and rehabilitation of floodplains resulted in the recovery of several waterbird species in Cameroon (Scholte 2006).

Detection of African woolly-necked storks in surveyed wetland habitats varied among season possibly due to expected annual variation in precipitation and temperature in KwaZulu-Natal. The winter in KwaZulu-Natal is characterised by low temperatures and the lack of rainfall which results in reduced food availability for this species in natural habitats (Hiestermann and Rivers-Moore 2014). These shortages of food sources associated with dry season might be the reason for lower detection probability and this could influence the

migratory behaviour of this population. The African woolly-necked storks are considered to no longer migrate in South Africa thus their status has been changed to non-migrant (del Hoyo et al. 2018). It is important to note that the suburban population of the African woolly-necked stork indeed occupies residential areas/human households, utilising anthropogenic food all year round (Thabethe and Downs 2018). Therefore, the population of this species in natural/rural wetlands might be locally migrating to suburban areas in winter, especially for food. A high abundance of prey in urban areas supports year-long residency among urban female Cooper's Hawks, whereas nearly all exurban females migrate (Mannan et al. 2008). Furthermore, the white stork, which was wholly migratory in Europe, has established resident populations because of guaranteed, year-round food from landfill sites (Gilbert et al. 2016). It will be of interest to attach radio-transmitters on the African woolly-necked storks to further determine their migratory status in South Africa, especially for the respective urban and rural populations.

Our study revealed that land cover change had negative effects on the occupancy of African woolly-necked storks. This was contradictory to our prediction that the change in land cover increased wetland occupancy, given that this species is widespread in urbanised areas. Local extinctions appeared to be offset by colonisation of unoccupied sites such that their range occupancy for 26 years was relatively stable. The colonisation and extinction probabilities were driven by anthropogenic development along with area of wetland, as well as wetland type. We found that as area of wetland increased, both colonisation and extinction increased. This provided evidence that the African woolly-necked stork both colonised wetlands and went locally extinct on a regular basis. The probability of colonisation increased with anthropogenic development while the probability of extinction decreased. Our results contradicted the traditional view that only natural wetlands far away from human disturbance support high colonisation of African woolly-necked storks. Both agricultural and urban habitats may have some direct benefit for African woolly-necked storks. Agricultural fields may increase the

abundance of invertebrates which are a major food source for African woolly-necked storks in adjacent wetlands (del Hoyo et al. 2018). Moreover, runoffs from irrigation canals have created patches of emergent marsh that are used by African woolly-necked storks in South Africa (Pers. Obs.). Several other storks are utilising agricultural fields adjacent to wetlands for foraging (Sundar 2006). The African woolly-necked stork also successfully exploits anthropogenic resources found in urbanised land in South Africa (SABAP2 2018). Consistent with our expectations, we found that occupancy of African woolly-necked storks was positively associated with wetlands area, though the relationship was not strong enough to conclude if these were true determinants of occupancy. This provides support for the argument that the value of a wetland increases with its size.

On observing the difference in land cover change or no change between two-time periods, several wetlands experienced change in land cover since 1990 in our study. The colonisation probabilities of African woolly-necked storks decreased with change in land cover. Our study suggests that population persistence after establishment was more dependent on the intensity of recent anthropogenic development rather than change in land cover. African woolly-necked stork populations may have thus taken advantage of recent anthropogenic development. African woolly-necked storks were found to inhabit wetlands of almost any sort, including estuaries, man-made dams, lakes, pans, rivers and wastewater treatment plants. This species is also usually sited close to swimming pools and pond in gardens (Thabethe and Downs 2018). Historically, however, the African woolly-necked storks' natural foraging preference has been for natural habitats. Okes et al. (2008) found that the main factor determining local colonisation or extinction of waterbird species in southern Africa was the use or non-use of human-made habitat in the form of impoundments and sewage works. Species that expanded home range and colonised new habitats used human-made habitat, whereas species that decreased home range and became local extinct in some sites avoided man-made

wetland habitats. African woolly-necked storks highlight the importance of the use of human-made wetlands in facilitating range expansion. This species was endangered in South Africa mainly due to habitat loss because it only occupied natural wetlands. The same species has expanded its range due to its use of man-made large wetlands such as wastewater treatment plants. Contrary to our prediction, wetland status and wetland areas did not have a strong influence on wetland occupancy of African woolly-necked storks, possibly suggesting that wetland type is more important than protected sites. We provided new information on the occupancy and habitat associations of African woolly-necked stork and its primary wetland habitats across KwaZulu-Natal.

This study highlighted the value of utilising data from long-term citizen science monitoring programs, such as CWAC, to determine trends and identify factors underlying long-term occupancy, colonisation and extinction of many other waterbird populations in South Africa. Dynamic occupancy modelling offers new developments for population studies and innovative applications of data from long-term citizen science monitoring program. Understanding the influence of land change on waterbird populations is critical to inform biodiversity conservation efforts. A particularly important goal is to understand how anthropogenic development density affects the persistence of bird populations through time, and how these impacts can be mediated by habitat provision.

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CHAPTER 3

Citizen science reveals widespread supplementary feeding of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa

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Running header: Supplementary feeding of African woolly-necked storks

3.1 Abstract

African woolly-necked storks (*Ciconia microscelis*) depend on wetland habitats for foraging and nesting in natural environments. Recently, they have started colonising urban environments in KwaZulu-Natal, South Africa, and are now a common sight in suburban areas in particular. There have been some anecdotal reports on supplementary feeding of this species by households in some urban areas where they are common. However, these reports have never been confirmed and therefore the extent of feeding and lack thereof is unknown. Using a questionnaire survey, we therefore investigated the extent (if any) to which householders in urban and suburban areas of KwaZulu-Natal provide supplementary food to African woolly-necked storks. We also determined the feeders' provisioning habits and identified the motivation behind and attitudes toward feeding. We found that a significant number of householders fed African woolly-necked storks on a daily basis throughout the year. The majority of respondents provided meat while others provided inappropriate food such as bread. Respondents were most often motivated to feed for personal pleasure. Our results showed that this species is successfully utilising and exploiting anthropogenic food – a novel behaviour. The observations and narratives from respondents strongly suggest that the African woolly-necked stork is present throughout the year, contrary to the perception that this species is migratory during winter. Based on the results obtained in this study, supplementary feeding of African woolly-necked stork by householders is relatively common, widespread and established in suburban areas of KwaZulu-Natal, South Africa. However, reported inappropriate feeding may create concerns regarding the health status of African woolly-necked storks in urban population. Therefore, to prevent further detrimental effects and potential human-wildlife conflicts we recommend that suitable feeding guidelines be formulated.

Keywords African woolly-necked storks · Domestic gardens · Questionnaire survey · Supplementary feeding · Urbanisation

3.2 Introduction

The provisioning of supplementary food by households for wild animals, especially birds, (hereafter referred to as supplementary feeding in this study) is a widespread practise throughout the globe particularly in the Western world (Jones and Reynolds 2008; Orros and Fellowes 2015; Hanmer et al. 2016; Reynolds et al. 2017). This practise originally started as a humane response to the plight of malnourished birds during severe winters in the northern hemisphere but has since been adapted globally and it is now generally practised year-round (Jones and Reynolds 2008; Cox and Gaston 2016). Approximately 50 -75% households in many developed countries (including Australia, New Zealand, the United Kingdom and the United States of America) participate in supplementary feeding of wild birds on a regular basis at an estimated cost of billions of US dollars annually (Rollinson et al. 2003; Gaston et al. 2007; Hanmer et al. 2016).

Supplementary feeding has been highlighted as one of the main factors that enables certain vertebrate species, especially avian species, to persist in urban areas (Marzluff et al. 2001). For example, red kites (*Milvus milvus*) are now abundant and widely distributed in the United Kingdom owing to widespread supplementary feeding in domestic gardens (Orros and Fellowes 2015). Indisputably, supplementary feeding provides an extremely important reliable food resource to many suburban birds in most parts of the world (Jones 2011; Galbraith et al. 2015). Moreover, supplementary feeding is now seen as a necessary means for facilitating wild birds in urbanised areas (González et al. 2006). In addition, feeding of wild birds can promote human health and well-being (Galbraith et al. 2014; Cox and Gaston 2016). However, while this practice can bring positive benefits, there are also a number of negative impacts associated with it.

The primary concern regarding supplementary feeding is the possibility that fed birds might become dependent or reliant on human-provided food (Ishigame and Baxter 2007;

Plummer et al. 2015). Concerns over transmission of avian diseases among fed birds and the fear of fed birds losing foraging skills has also been highlighted (Jones 2011; Hanmar et al. 2016). Furthermore, the possibility of nutritional imbalance and malnutrition due to inappropriate food been provisioned is a concern for both opponents and advocates of bird feeding (Wilcoxon et al. 2015). Recent studies have provided evidence that the provision of supplementary food for wild birds in suburban areas increases the likelihood of local nest predators (Bonnington et al. 2015; Hanmer et al. 2016). Interestingly, it is strongly suggested that the benefits of supplementary feeding outweigh any negative impacts that may occur (Murgui and Hedblom 2017; Reynolds et al. 2017).

Whilst avian provisioning of supplementary food generally targets passerines with predominantly granivorous diets especially seeds, meat is also regularly provided to a number of large birds including the Australian magpie (*Gymnorhina tibicen*) (O’Leary and Jones 2006), rainbow lorikeets (*Trichoglossus haematodus*) (Gillanders et al. 2017) and red kites (Orros and Fellowes 2014; Orros and Fellowes 2015). Although the practise of supplementary feeding of wild birds is common and well-studied in the developed world, relatively little is known about it in Africa. More surprisingly, there is no published information on supplementary feeding of wild birds in South Africa despite the practice being popular in relatively wealthy neighbourhoods (Reynolds et al. 2017). Recently, there have been some anecdotal reports on direct supplementary feeding by humans of African woolly-necked storks (*Ciconia microscelis*) in some urban areas of South Africa. However, these reports have never been confirmed and therefore the extent of feeding and lack thereof is unknown. Therefore, the aim of our study was to investigate the extent (if any) to which householders in urban and suburban areas of KwaZulu-Natal provide supplementary food to African woolly-necked storks. We also determined the feeders’ provisioning habits and identified the motivation behind and attitudes toward feeding (human-wildlife interaction). In doing so we hoped to discern the incidence of

harmful practises and assist with formulating appropriate feeding guidelines for those involved in feeding.

3.3 Methods

Study areas

Our surveys were conducted around KwaZulu-Natal Province (Fig. 3.1), which lies on the eastern seaboard of South Africa. According to population dwelling counts, KwaZulu-Natal contains the second largest human population of the nine provinces of South Africa (Statistics South Africa 2007). The main cities that we focused on were Durban, (within eThekweni Municipality located on the east coast: 29°85'85. 30", 31°02 '60. 02) and Pietermaritzburg (within Msunduzi Municipality located in the midlands area: 29°34'48. 82" 30°22'26. 91). Durban is the largest city in the province while Pietermaritzburg is the second largest (Statistics South Africa 2007). The physical geography of these cities are mosaics of human-modified habitats of different housing and industrial densities characterised by diverse societies of different social and economic standards and with varieties of natural greenbelts and conservancies interspersed among them. The housing range includes human informal settlements, suburban residences and dense urban living spaces (McPherson et al. 2016a,b). Both cities have developed rapidly over the recent decades (McPherson et al. 2016a,b; Singh and Downs 2016). KwaZulu-Natal has a subtropical climate that makes it ideal habitat for several bird species and wildlife (McPherson et al. 2016a,b). The African woolly-necked storks are mainly sighted around these municipalities, particularly in the suburban areas (SABAP2; Thabethe and Downs unpublished data).

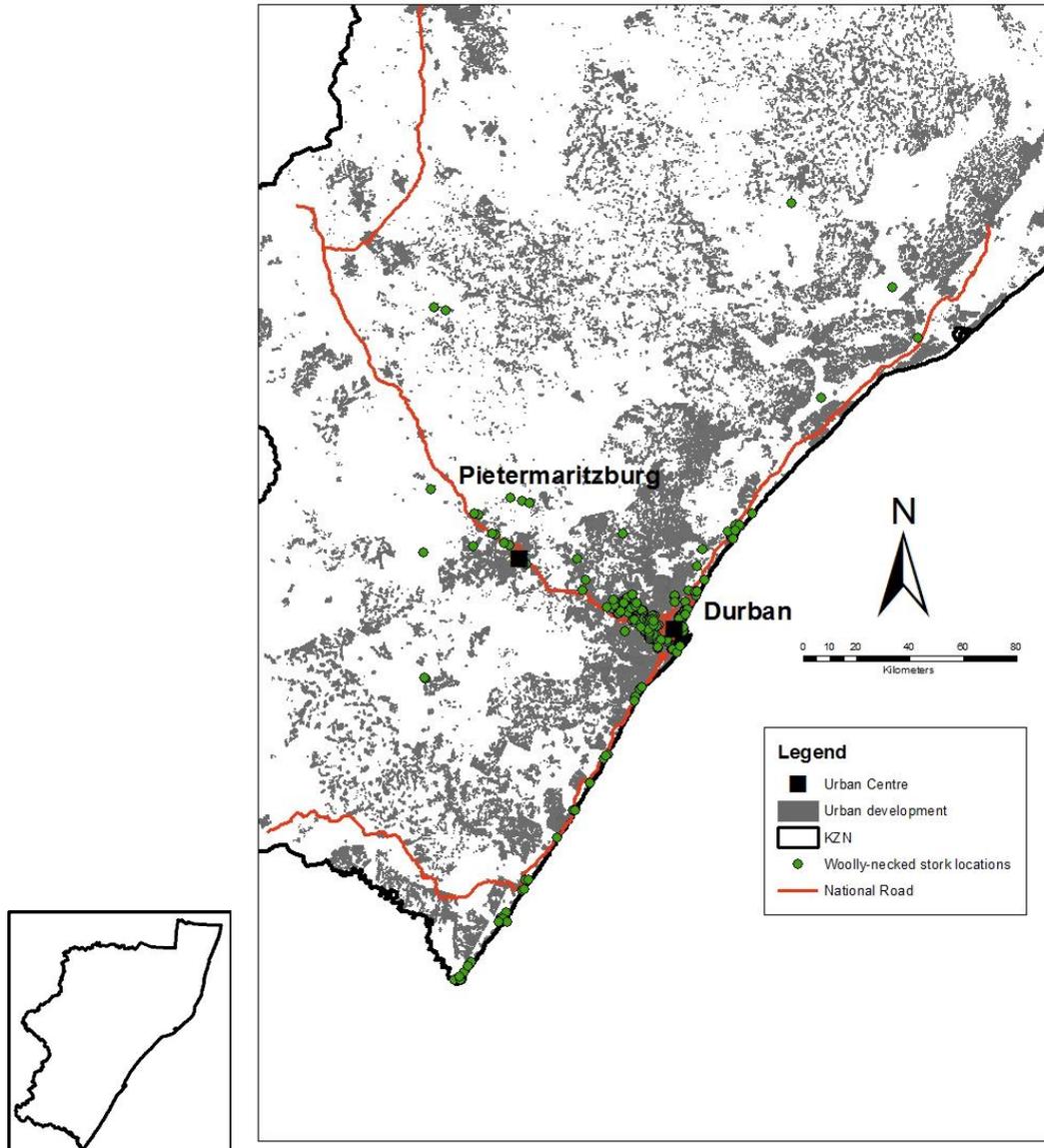


Fig. 3.1 Location of the municipalities (inclusive of eThekweni and Msunduzi) of which surveys were conducted in the KwaZulu-Natal Province, South Africa. (Dots represent both feeding and non-feeding households that participated in this study).

Study species

The African woolly-necked stork (*C. microscelis*), previously known as the woolly-necked stork (*C. episcopus*) (del Hoyo et al. 2014) is a relatively large wading bird which belongs to the *Ciconiidae* family and is indigenous to sub-Saharan Africa (Cyrus and Robson 1980). In the wild, they feed on amphibians, insects, small mammals and reptiles. The African woolly-

necked stork was previously a scarce visitor to KwaZulu-Natal (Clancey 1964; Cyrus and Robson 1980; Allan 2012). The first breeding pairs of the African woolly-necked stork in KwaZulu-Natal were reported in the 1950s and 1960s (Clancey 1964; Cyrus and Robson 1980). By the late 2000s African woolly-necked stork numbers had increased considerably in KwaZulu-Natal leading to their delisting from endangered red list to least concern species in 2004 (SABAP2). The African woolly-necked stork has since increased its range dramatically and today occupies man-made habitats including golf courses, sport fields, parks, cemeteries and domestic gardens in many suburban areas of KwaZulu-Natal (SABAP2; Thabethe and Downs unpublished data). KwaZulu-Natal Province has the highest number of African woolly-necked storks in South Africa (SABAP2).

Data collection and participant recruitment

From March 2014 an article requesting observational information of African woolly-necked storks was widely distributed via local newspapers, email circulation and advertisements at community meetings to suburban residents of Ethekewini and Msunduzi Municipalities. The article specifically asked for the date, time, geographical location (Global Positioning System points (GPS) coordinates) and photographs of any direct visual sightings of African woolly-necked storks anywhere in KwaZulu-Natal. Photographs of the African woolly-necked stork were included in the newspaper articles to aid in the correct identification of the species. A total of 418 people responded to the newspaper articles. A questionnaire was then distributed to all the respondents, of which 234 (56%) questionnaires were returned. The main section of the questionnaire aimed at collecting quantitative data relating to the extent of African woolly-necked stork supplementary feeding and information relating to what food was provided, how often, what time of the year, how it was provided and what were the motivations behind the feeding (Supplementary Appendix S3.1). Questions included dichotomous questions (yes/no),

multiple choice questions and open-ended questions (Supplementary Appendix S3.1). Many respondents went beyond the scope of observational questions providing more historical information on the species based on their personal observations and experiences.

Non-responses to some questions occurred within some of questionnaires. Only the given responses were analysed in this study. This study had University of KwaZulu-Natal ethical clearance, which complied with the ethical standards of the relevant national and institutional committees on human experimentation and with the Helsinki Declaration of 1975, as revised in 2008 (Protocol number HSS/0947/012M).

Statistical analyses

Owing to the exploratory nature of this study, only descriptive statistics and non-parametric statistics were conducted in this study. All statistics were performed in Statistica (StatSoft, Tulsa, OK, 2006).

3.4 Results

Supplementary food provision for African woolly-necked storks

Most (71%, 165 respondents) respondents indicated that their household engaged in African woolly-necked stork supplementary feeding. The majority of respondents (63.4%) provided meat (Fig. 3.2) to storks. Chicken was the meat most provided by respondents (50.7%, Fig. 3.2), while red meat was provided by only 12.7%. Chicken livers, necks and hearts were the most popular parts of chicken provided to storks (Fig. 3.2). Most (98%) of the respondents provided raw meat while only a few (2%) provided processed meat. A number of respondents provided cheese (21%) while some respondents provided bread (9%), and dog or cat food (5%) for storks. Only three respondents provided both leftover food and mealworms (*Tenebrio* spp.) for storks. Seventy-three percent (73%) of respondents provided more than three types of food, with just twenty-seven percent (27%) providing one type of food daily for storks. A

considerable number of respondents stated that they spend money on food specifically for African woolly-necked storks (86%), while relatively few (14%) (mainly those feeding bread and leftovers) did not spend any money on food specifically for storks but fed what they had available. It was difficult to quantify the amount of supplementary food consumed by African woolly-necked storks per day because of the range of food provided and the differences in the way it was presented.

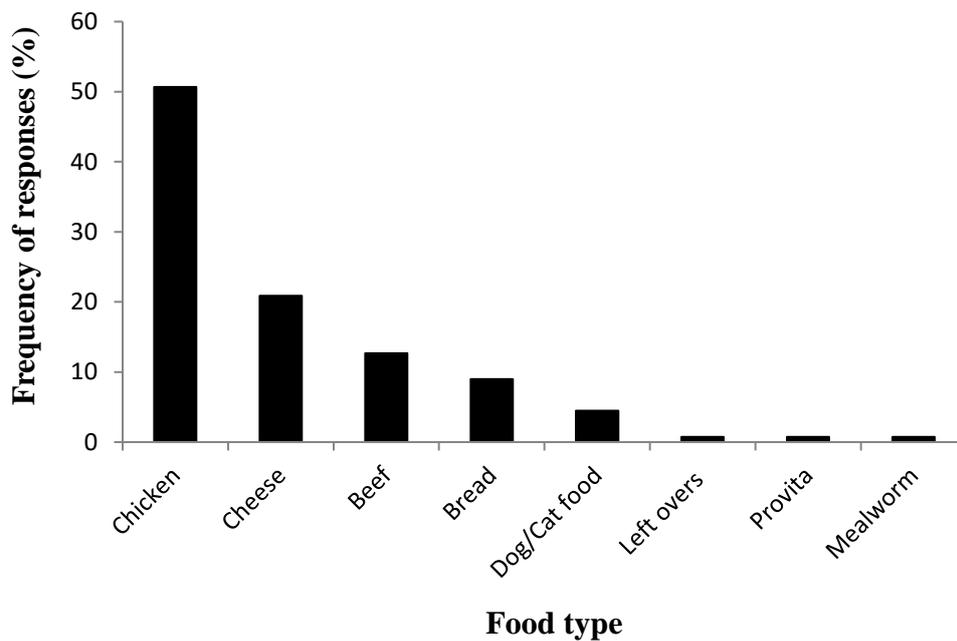
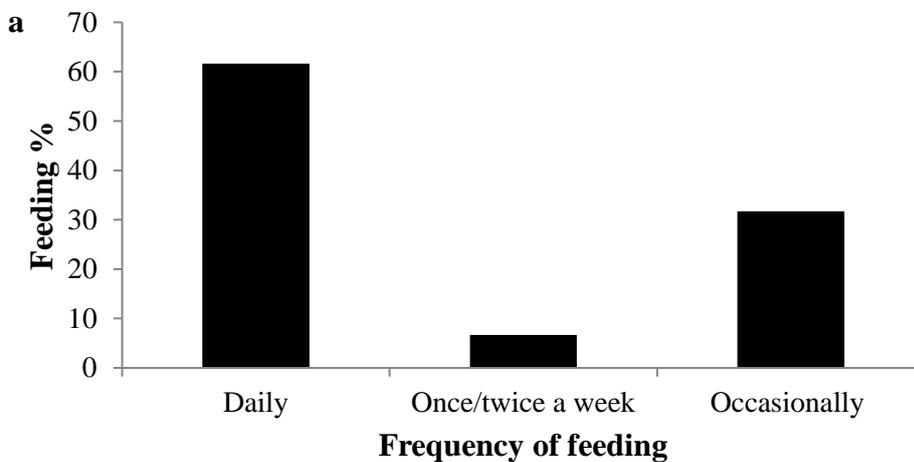


Fig. 3.2 Frequency of the various different food types provided to African woolly-necked stork as supplementary food by households in Pietermaritzburg and Durban, South Africa (n = 165).



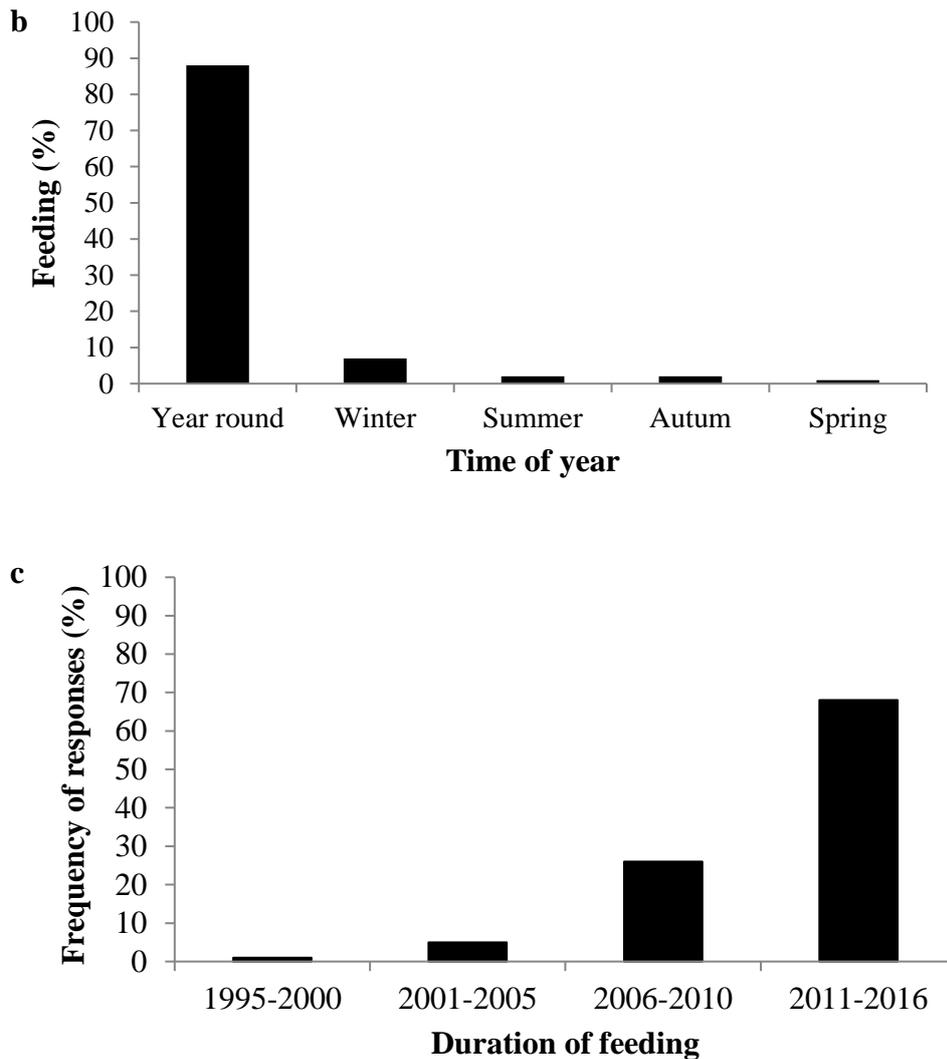


Fig. 3.3 Supplementary feeding of African woolly-necked storks where (a) is frequency of feeding, (b) seasonality of feeding, and (c) year of commencement of feeding of African woolly-necked storks reported by respondents from KwaZulu-Natal suburban areas.

Duration, seasonality and frequency of feeding

African-woolly-necked stork supplementary feeders were asked how often they fed and how long that they been feeding storks to gain further insight into the extent of supplementary feeding, especially in urban areas. The majority of respondents (88%) provided supplementary food for the storks throughout the year while a small minority (12%) fed only at certain periods of the year, or whenever the study species was around (Fig. 3.3b). Of respondents who provided

food at a specific time of the year, few fed only in winter (9%) while fewer fed only in summer (3%) (Fig. 3.3b). Sixty two percent (62%) respondents indicated that they provided supplementary food for storks daily; only seven percent (7%) provided food once or twice per week, with the remainder (31%) stating that food was only provided occasionally (Fig. 3.3a). Most (61%) of African woolly-necked stork daily feeders fed only once a day while 39% fed more than once a day throughout the year. The majority of those feeding once a day fed in the morning (90%). The length of time respondents had been feeding African woolly-necked storks varied; most respondents started feeding from 2011 (68%) while some started feeding from 2006 (26%) and only a few (6%) fed prior to 2005 (Fig. 3.3c).

Motivation for feeding

The most common reason for supplementary feeding of African woolly-necked storks given by respondents feeding them was that the practice brought them pleasure (85%). Many respondents indicated that it was a privilege to be visited by African woolly-necked storks as it was once a rare species in South Africa. Furthermore, many enclosed photographs and went to considerable lengths to convey the joy they experienced in feeding African woolly-necked storks. Other respondents fed African woolly-necked storks to facilitate their survival in urban areas and to see them up close while (11%) some fed them to assist this species with reliable food sources to compensate for habitat destruction caused by humans (4%). Overall, respondents agreed with the practice of feeding African woolly-necked storks with the desire to conserve them. All respondents were pleased with the recovery and occurrence of African woolly-necked storks in KwaZulu-Natal. Respondents who did not feed African woolly-necked storks mostly stated that they were concerned about the storks' welfare and were afraid that they might become dependent on humans for food.

Attachment and ownership

Some respondents had given pet names to the African woolly-necked storks that they fed regularly (12%). For example, one respondent wrote “Alfred and Rema love cheddar cheese”, another responded wrote “Wally and Wilamena have been visiting me for a couple of years now and this year they brought their baby”. Furthermore, many respondents referred to the storks as “my” stork and went on to say they had a special relationship with their particular storks (27%). This was interpreted as a sense of claiming ownership of the visiting African woolly-necked storks. A number of people sent pictures of African woolly-necked storks feeding directly from their hands and entering inside their living rooms or kitchens in search of the supplementary food (7%) (Fig. 3.4a and b). Some respondents even claimed that the storks recognised their voices (5%). Almost all respondents stated that African woolly-necked storks were tolerant of humans and were tame (89%). Many respondents gave extensive details of their observations and interactions with African woolly-necked storks and expressed a sense of wonder when describing their relationship with the visiting storks (65%).

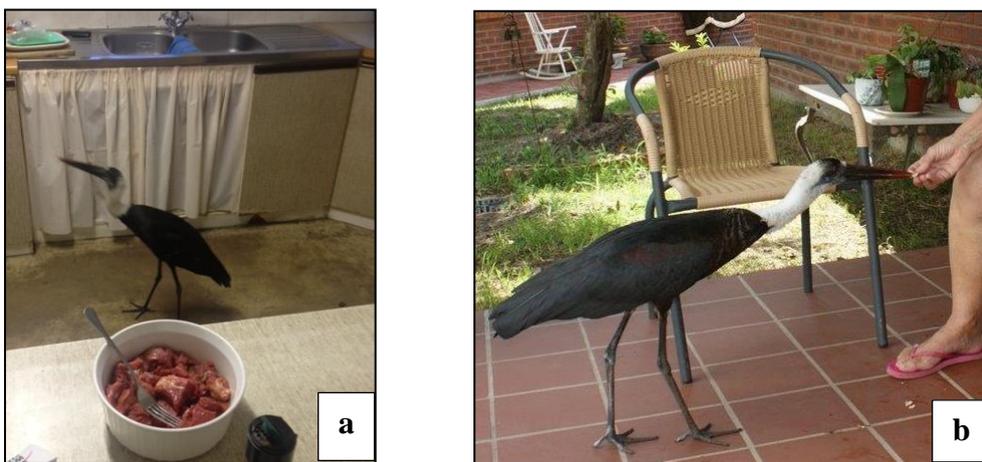


Fig. 3.4 Incidents of African woolly-necked storks in close contact with humans showing feeding (a) inside a kitchen of a home, and (b) from the hand, in suburban gardens in KwaZulu-Natal

Concerns associated with feeding

As mentioned, some respondents who were not feeding African woolly-necked storks were concerned that supplementary feeding might make the storks dependent on humans (33%). Others raised the concern of diseases transmission due to unhygienic feeding stations and feeding of inappropriate food that might negatively impact the health of the fed species (16%) (welfare of the urban population). Some supplementary feeding respondents were concerned about whether they were feeding appropriate food and asked for our opinions as there were no available guidelines (47%). Of great concern were the number of African woolly-necked storks ($n = 45$) reported and/ or recorded with leg or foot damage either evident as leg deformities, or as injuries from fishing line (Fig. 3.5). Some individuals had one or several phalanges missing from their feet (pers. obs.).

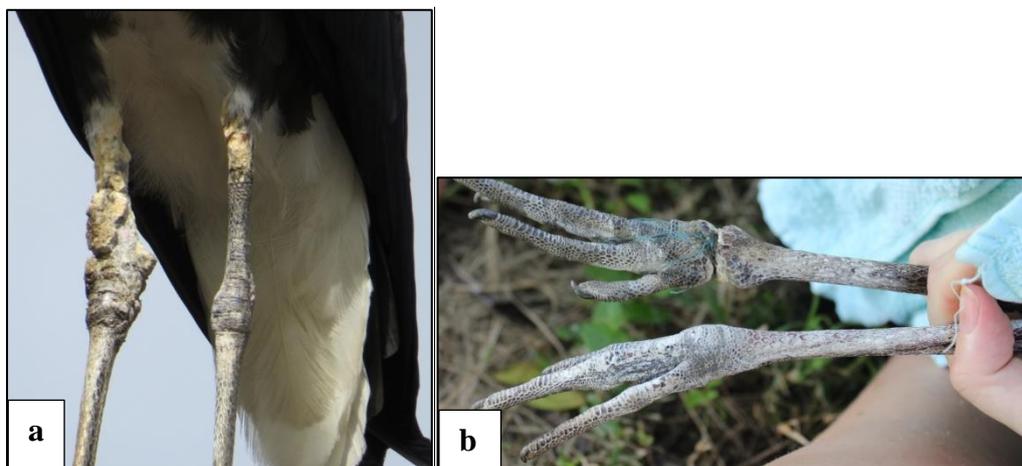


Fig. 3.5 Incidents of African woolly-necked storks showing leg damage where (a) shows an individual with a leg deformity, and (b) an individual with injuries from fishing line, in suburban gardens in KwaZulu-Natal

3.5 Discussion

The questionnaires were completed mainly by individuals (n = 234) who contacted us in response to our request for African woolly-necked stork sighting data on social media and in newspapers in KwaZulu-Natal. Of these 71% (n = 165) confirmed supplementary feeding of African woolly-necked storks. These data provided the first evidence that supplementary feeding of this species is common and widespread in urban areas of KwaZulu-Natal, South Africa.

Our study revealed that many urban inhabitants provide supplementary food for African woolly-necked storks in their domestic gardens and had succeeded in attracting them as regular visitors. We found that 71% respondents deliberately fed African woolly-necked storks in their households, with most respondents feeding on daily basis. There is no evidence from previous records to suggest that African woolly-necked storks utilised and/or exploited anthropogenic resources historically (Cyrus and Robson 1980). It is appropriate, therefore, to view the utilisation of artificial food by African woolly-necked stork as a novel behaviour that has developed in recent years. The African woolly-necked stork is not the first stork to successfully colonise urbanised habitats: the white stork (*Ciconia ciconia*) and the marabou stork (*Leptoptilos crumenifer*) are flourishing in urban areas of Europe and Africa respectively, almost certainly owing to the relative ease access to anthropogenic food, particularly from waste landfill sites (Van den Bossche et al. 2006; Martin et al. 2010; Hilgartner et al. 2014; Djerdali et al. 2016; Gilbert et al. 2016; Pomeroy and Kibuule 2017). However, we are not aware of deliberate provisioning of other storks by urban householders, although other meat-feeding birds are fed in Australia (O’Leary and Jones 2006) and Britain (Orros and Fellowes 2014; Orros and Fellowes 2015). Recently, rainbow lorikeets have also been reported to consume meat at feeding stations in Australia (Gillanders et al. 2017).

Encouragingly, we found that 63% of the African woolly-necked storks' supplementary feeders provided meat, with the majority providing raw meat that contained skin and/or bone. Fortunately, meat is considered as appropriate food for carnivorous birds such as red kite (Orros and Fellowes 2014) and the Australian magpie (O'Leary and Jones 2006). However, it was of concern that some respondents provided inappropriate food such as cooked meat, processed meat and bread. Processed food has been shown to have calcium deficiencies and harmful additives which may lead to serious bone disorders while cooked meat may cause dietary deficiencies (Galbraith et al. 2014; Ewen et al. 2015). Bread has been strongly associated with digestive problems which may lead to lactic acidosis in birds (Rollinson et al. 2003). Of concern were the number of African woolly-necked storks reported with damaged or deformed legs and/ or feet either from possible malnutrition or from injuries caused by anthropogenic objects or litter. Deformed birds have been observed elsewhere, for example common eiders (*Somateria mollissima*) were reported with abnormalities of their legs, feet and beaks which are thought to be associated with environmental contaminants (Weatherhead 1979).

Motivations for people feeding African woolly-necked storks were mainly centred on personal enjoyment. Providing food for African woolly-necked storks provided pleasure and joy to many supplementary feeding respondents. Other studies have similarly found that one of the main motivations for supplementary feeding is the pleasure it generates (e.g. Howard and Jones 2004; Orros and Fellowes 2015). Evidence suggests that feeding wild birds gives people an increased sense of psychological well-being because it provides them with a feeling of being connected to nature (Jones 2011; Reynolds et al. 2017). Furthermore, several respondents fed African woolly-necked storks to promote their persistence and welfare with the perception that natural food was limited in urban areas. Overall, respondents expressed a high level of appreciation for African woolly-necked storks.

It was not surprising that that the most common reason for some respondents not feeding African woolly-necked storks, was the issue of potential dependency on supplementary feeding. Other studies have similarly found that the issue of dependence is probably the most cited concern regarding supplementary feeding of wild birds worldwide (Galbraith et al 2014; Reynolds et al. 2017), although some studies strongly suggest that there is no evidence of birds becoming significantly reliant on supplementary feeding (Jones 2011; O’Leary and Jones 2006; Wilcoxon et al. 2015). While many African woolly-necked storks did utilise supplementary feeding in suburban gardens extensively, they continued to forage for natural food in nearby lawns, recreation areas (such as golf courses) and natural open spaces suggesting that in addition they still forage naturally (Thabethe and Downs unpublished data). Well-watered short lawns in urban areas also provide an ideal foraging habitat for several wading bird species in KwaZulu-Natal regardless of season (Singh and Downs 2016; pers. obs.).

There was an obvious emotional attachment to African woolly-necked storks among supplemental feeders with many respondents expressing a strong feeling of protection and commitment to provide assistance and care for ‘their’ birds. Similarly, a sense of ownership over wild birds has been reported in Australia where respondents have used word such as ‘my’ referring to birds that they feed (Howard and Jones 2004). Numerous detailed reports from supplementary feeders as well as our own observations support that African woolly-necked storks are relatively domesticated in urban areas of KwaZulu-Natal, with some even feeding from the hand and others going inside homes to find the supplemental food.

Interestingly, one respondent raised concerns about African woolly-necked stork damaging her ornamental flowers and hoped that they would not be a nuisance in the future with their numbers increasing in urban areas. Although this was the only negative encounter reported, high densities of African woolly-necked storks in urbanised habitats may cause increased negative encounters in the future which may result in many people losing tolerance

of the species and leading to increased human-wildlife conflict. It is worthwhile to remember that many of today's nuisance/problematic birds in urban areas were once encouraged by urban residents. African woolly-necked storks also utilise suburban rooftops for roosting and perching (Thabethe and Downs unpublished data), depositing their excreta on rooftops which may cause further human-wildlife conflict in the future. It is therefore suggested that the population of this species should be monitored and potentially managed to reduce human-wildlife conflict.

The widespread supplementary feeding of African woolly-necked storks in suburban areas of KwaZulu-Natal is interesting because the activity is controversial. For instance, increased availability of food might increase reproductive success and therefore increase fledgling populations which may be a tool to attenuate population loss caused by habitat degradation. Reproductive success of white storks was significantly higher in pairs breeding in close proximity to a feeding site (Hilgartner et al. 2014). However, supplementary feeding of African woolly-necked storks might also increase disease prevalence and increase nutritional imbalances thus causing higher mortality rates. Wilcoxon et al. (2015) reported increased disease prevalence in birds where supplementary food was offered. Some authors have also provided evidence that supplementary feeding for wild birds may increase the risk of nest predation (Bonnington et al. 2015; Hanmar et al. 2016). However, as African woolly-necked storks generally nest away from the areas where they receive supplementary feeding (pers. obs.) attracting their potential nest predators is unlikely. It will be important to assess whether supplementary feeding affects the overall nesting success of African woolly-necked storks positively.

Although determination of African woolly-necked storks' seasonal movements was beyond the scope of the current study, it was interesting to learn that the majority of respondents supplementary fed throughout the year, showing that a non-migratory population of African

woolly-necked stork have established in suburban and urban areas across KwaZulu-Natal. This concurs with the Gilbert et al. (2016) study, which showed that the continuous availability of food resources in waste landfill sites has influenced the home ranges and movement behaviour of white storks in the United Kingdom. Given the length of time that many respondents claim to have been undertaking supplementary feeding of African woolly-necked storks, the level of their dedication to this and the likely amount of money they spend on supplementary food showed that the presence of African woolly-necked storks were an important part in the lives of most respondents (possibly adds considerably to a respondent's quality of life) and that their provisioning behaviour was likely to continue.

The African woolly-necked stork is an interesting species: having been largely absent from urbanised habitats until the late 1990s, this species is now thriving in urban areas of South Africa (SABAP2; Thabethe and Downs unpublished data). The African woolly-necked stork was removed from the endangered bird list to least concern species in 2004 (Birdlife International 2017). The migratory status of this species has also been changed to non-migrant (Birdlife International 2017). This species is now commonly observed and successfully breeding in suburban areas, mainly in private domestic gardens, in KwaZulu-Natal (Thabethe and Downs unpublished data). Globally this is the only stork species that appears to respond positively to direct human supplementary feeding. They also frequent waste landfill sites (Thabethe and Downs unpublished data) as do white storks and marabou storks (Van den Bossche et al. 2006; Martin et al. 2010; Hilgartner et al. 2014; Djerdali et al. 2016; Gilbert et al. 2016; Pomeroy and Kibuule 2017). We speculate that predictable provisioning of supplementary food by humans in gardens within suburban areas of KwaZulu-Natal has influenced the local abundance, year-round presence, and distribution of the African woolly-necked stork here (SABAP2; Thabethe and Downs unpublished data)

Conclusion

This study provides first confirmation of widespread supplementary feeding of African woolly-necked storks by householders in KwaZulu-Natal suburban areas which has resulted in the storks becoming permanent residents in these areas. Consequently, this species which is naturally carnivorous feeding primarily on amphibians, reptiles, and small mammals, is now an opportunist feeder and a scavenger. This shows their behavioral flexibility and adaptability to the kind of supplementary foods available in suburbia. Of concern were the cases of inappropriate food been fed to African woolly-necked storks and the number of incidences of them having leg deformities. This study highlights that without information about ecological consequences, humans may unintentionally make harmful choices for African woolly-necked storks. Our study seeks neither to promote nor to discourage supplementary feeding of African woolly-necked storks but to provide baseline information on the extent of feeding and type of food provided which will be important in formulating suitable feeding guidelines. To our knowledge, this is the very first study on supplementary feeding of African woolly-necked storks in South Africa.

3.6 Acknowledgements

We are grateful to numerous members of the public who kindly replied to our sighting request and those who completed our questionnaire. Special thanks to MM Zungu and MB Khambule for their valuable input on the manuscript. We thank the University of KwaZulu-Natal, the National Research Foundation (ZA) and the Rufford Foundation (GB) for funding. We also thank Idea Wild (US) for donating binoculars and a laptop. We thank the editors and anonymous reviewers for their constructive comments that greatly improved the final manuscript.

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Appendix S3.1

Supplementary Appendix S31: Questionnaire on Woolly-necked storks in suburban neighbourhoods

Thank you for taking the time to complete this survey. This survey is for information purposes only. Please try to answer all questions to the best of your knowledge and be as accurate as possible.

This research forms part of a study of African woolly-necked storks in suburban/urban areas currently been undertaken in the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg campus.

- 1. Do you feed African-woolly-necked storks in your garden?**
Yes / No

If no:

- 2. Why are you not feeding?**

If yes:

- 3. How often do you feed African woolly-necked storks?**
More than once a day / Once a day / A few times a week / Weekly/ Monthly/ Other
(Please specify)

- 4. What time of the day do you feed?**

Early morning (06h00 – 10h00), Midday (12h00 – 14h00), Afternoon/Evening (14h00 – 18h00), Other (Please specify)

- 5. What time(s) of year do you feed African woolly-necked storks?**
Year round, Spring, Summer, Autumn, Winter Other (Please specify)

- 6. What types of food do you feed? Please write your answer below**

- 7. Do you feed raw or cooked food? Please write your answer below**

- 8. Where do you put the food?**

On the ground, Open dish/plate, Open bird table, Other (specify)

- 9. Approximately how long have you been feeding African woolly-necked storks?**
Please write your answer below

- 10. Do you spend money on food specifically for African woolly-necked storks?**

Yes/No

- 11. Why do you feed African woolly-necked storks? Please write your answer below**

- 12. If you no longer feed African woolly-necked storks, why did you stop? Please write your answer below**

- 13. Do you agree with feeding wild birds?**

Yes, No, Undecided

14. Further comment? Please write below

Thank you, your participation is greatly appreciated.

CHAPTER 4

Nest site selection of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa

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Submitted to the Urban Ecosystems

Running header: Suburban nest sites of African woolly-necked storks

4.1 Abstract

Rapid urbanisation is a global phenomenon that is generally a threat to biodiversity. Habitat loss has been identified as a primary threat to African woolly-necked storks (*Ciconia microscelis*). However, this species has successfully established breeding sites in suburban areas of KwaZulu-Natal (KZN), South Africa. Understanding landscape features of suburbia that promotes their occupancy may become important for conservation management strategies for persistence of this species. From 2015-2017, we located 30 African woolly-necked stork nests in suburban areas of KZN. By comparing used nest sites to randomly chosen non-used nest sites, we determined which features of the nest tree and surrounding habitat influenced their nest-site selection. We found that they have successfully established breeding sites in areas of human habitation, especially near swimming pools and occupied residences, while exotic pine (*Pinus elliottii*) and eucalyptus (*Eucalyptus spp.*) trees were the most preferred

trees. All nest trees were taller, and of greater diameter when compared with random sites. Anthropogenic structures were also used as nesting sites. Levels of human disturbance did not appear to influence nest-site selection. This was contrary to previous research that they only nest in natural wetlands habitats. Presence of African woolly-necked storks in suburban areas of KZN was associated with the availability of tall trees, abundance of artificial water sources and accessibility to food, especially supplementary feeding by households. Their nesting behaviour shifts may also aid them to adapt to suburban areas. For successful long-term conservation of African woolly-necked storks, it is crucial that the existing nesting trees are protected.

Keywords: nest sites · suburban residential · stork · urban wildlife · tree availability · breeding behaviour

4.2 Introduction

Urbanisation is rapidly increasing across the globe and is considered as a major threat to biodiversity due to habitat loss or fragmentation (Lowry et al. 2012). Globally, urbanisation is regarded as one of the leading causes of species extinction (Faeth et al. 2005; Kopij 2017). Despite this, some avian species persist in urban areas and their populations may reach higher densities than in natural habitat (Dawson and Mannan 1994; Boal and Mannan 1998; Lowry et al. 2012; Tripathi 2016; Kopij 2017; Smith et al. 2017; Chaudhury and Koli 2018). This phenomenon could be attributed to these abilities to adapt to some landscape features of urbanisation (Minias 2016). Several nesting behavioral adaptations to urbanisation have been documented in a wide range of bird species (Singha et al. 2002; Tripathi 2016). These include shifts in nest sites from natural places to anthropogenic structures (Vaghela et al. 2015; Wang et al. 2014) and adjustment in the height at which the nest is built (Wang et al. 2008). A number

of factors are likely to influence nest site selection in birds breeding in suburban areas, including close proximity to food sources, tree structure and level of disturbance around the nest (Soh et al. 2002; Ishtiaq et al. 2004; Kopij 2017). Additionally, certain species select nest sites primarily to reduce nest predation (Jokimaki and Huhta 2000; Vincze et al. 2017) while other select sites to reduce negative effects of weather (Roshnath and Sinu 2017). Many studies suggest that bird species are highly selective in their choice of nest site (Hartman et al. 2016; Winiarski et al. 2017; Zhang et al. 2017). Selection of appropriate nest sites is of importance as it has major implications on reproduction success and survival of bird species (Onmus et al. 2012; Tobolka et al. 2013; Vaitkuvienė and Dagys 2015). Therefore, it is important to understand nest-site selection in avian species occupying urbanised environments to inform appropriate conservation management strategies for conserving and/or restoring features of the environment that support species persistence and recovery.

Although African woolly-necked stork (*Ciconia microscelis*) populations have seen strong recovery (SABAP2 2018) especially in suburban areas of KwaZulu-Natal (KZN), South Africa, since listing under the Endangered Species List (Birdlife International 2018), no scientific studies have been conducted on features in suburban areas that determine nest site selection and nesting behaviour that promote occupancy of this stork species in such novel environments. Naturally, the African woolly-necked stork is highly dependent on wetlands (del Hoyo et al. 2018). African woolly-necked storks originally built nests in natural wetlands, mainly on overhanging trees far away from disturbance (Clancey 1964). Loss of breeding habitat, especially due to urbanisation and human disturbance, is the primary threat to populations of African woolly-necked stork (Clancey 1964; Cyrus and Robson 1980; Allan 2012). However, African woolly-necked storks have successfully established breeding sites in suburban areas of KZN (SABAP2 2018). Factors influencing nest site selection of African woolly-necked storks in suburban areas are not known. The on-going urbanisation and the

ability of African woolly-necked storks to persist in urban environments suggest that base-line data on habitat selection of this species is important for suburban planning and management. We therefore, studied nest site selection and nesting habit of African woolly-necked storks in KZN. Based on the natural requirements of African woolly-necked storks for suitable nest trees, we predicted that in the suburban environment, nest sites would be close to wetlands, on tall trees overhanging water while being further from roads and occupied houses than random locations. Understanding nest site selection and factors contributing to nesting success, especially in urban landscape, may allow managers to improve nesting habitat suitability and make informed decisions about potential effect of future developments.

4.3 Methods

Study species

The African woolly-necked stork occurs widely across Africa, from northern (e.g. Sudan) to sub-Saharan Africa (e.g. South Africa) (del Hoyo et al. 2018). It can occupy almost any wetland habitat including rivers, lagoons, dams, estuaries and impoundments (del Hoyo et al. 2018). The African population has been recently split from its Asian counterpart *C. episcopus* and assigned a specific status as African woolly-necked stork *C. microscelis* by BirdLife International (2018). Previously, African woolly-necked storks were more coastal in their distribution in South Africa (Cyrus and Robson 1980). However, their distribution ranges have expanded and are now sighted further inland (SABAB2 2018) especially in KZN. In our study areas, they frequent man-made habitats including golf courses, parks, domestic garden lawns, school grounds and other open spaces with short grass. This species mainly feeds on insects and other invertebrates mostly foraging by slowly walking through water and vegetation stabbing preys (del Hoyo et al. 2018). It also feeds on vertebrates including amphibians, reptiles and small mammals (del Hoyo et al. 2018). A recent study revealed that the African woolly-

necked stork is widely fed by households on regular basis usually throughout the year in our study area (Thabethe and Downs 2018). The supplementary food includes chicken, processed meat, cheese and bread (Thabethe and Downs 2018). African woolly-necked storks breed in solitary pairs and breeding pairs are monogamous. In the study area, breeding occurs between August and December (Clancey 1964; Cyrus and Robson 1980). They build large platform sticks nests with a central bowl lined with fine twigs and greenery on tall tree (Clancey 1964). The nest is typically placed 10-30 m (sometimes up to 50 m) above ground water (Cyrus and Robson 1980). Females usually lay 2-4 eggs and have a nesting cycle that includes incubation of up to 30 days and brooding period of 25-35 days (del Hoyo et al. 2018). Both parents are involved in building the nest, incubation and brooding (del Hoyo et al. 2018). The chicks are fed by both parents; food is regurgitated on the floor of the nest from the crop or stomach (del Hoyo et al. 2018). The nest material particularly greenery is delivered by both parents throughout the breeding season, up to the fledgling of chicks probably to keep it sanitary and clean (del Hoyo et al. 2018). The potential predators of African woolly-necked storks in our study area are Egyptian geese (*Alopochen aegyptiaca*), vervet monkeys (*Chlorocebus pygerythrus*), pied crow (*Corvus albus*) and yellow-billed kites (*Milvus aegyptius*) (Thabethe and Downs unpublished data).

Study area

This study was conducted in the cities of Durban (29°85'85. 30", 31°02'60. 02") and Pietermaritzburg (29°34'48. 82", 30°22'26. 91") in KZN, South Africa (Fig. 4.1). This region is characterised by the Indian Ocean Coastal Belt biome, conservancies and human-modified landscape of varying housing density including suburban residential areas, informal settlements (low income residents) and industrial areas. Suburban areas of KZN occur in mosaics often with relatively low-density housing with green open spaces nearby (McPherson

et al. 2016). Generally older suburban areas have relatively well established and sized domestic gardens with well-maintained lawns and some tall trees, with many have a swimming pool and/or water feature (pers. obs.), and sometimes supplemental feeding of wildlife (Thabethe and Downs 2018). These areas abut public open spaces including golf courses, cemeteries, parks and school grounds or have natural areas with rivers, grassland or forest nearby. Pietermaritzburg has a population of ~475,000 inhabitants (Statistics South Africa 2011) while Durban currently supports ~3.4 million citizens (Statistics South Africa 2011). KZN is one of the smallest provinces, yet it contains the second largest human population of the nine provinces of South Africa (Statistics South Africa 2011). Both cities have developed rapidly over the past decades (McPherson et al. 2016; Singh and Downs 2016). The subtropical climate of KZN makes the province ideal for a number of wildlife (McPherson et al. 2016). The African woolly-necked storks are mainly sighted in these two municipalities, particularly in suburban areas (SABAP2 2018; Thabethe and Downs 2018). KZN has the largest population of African woolly-necked storks associated with urban landscapes in South Africa (SABAP2 2018).

Nest site location and data collection

Surveys were conducted from April 2015 to December 2017 in KZN, with the most sampling effort between August and December each year during African woolly-necked stork courtship and nest building periods. Searching for African woolly-necked stork nest sites was conducted through public outreach, social networks and vehicle surveys. The public were requested to report any known nests through local newspaper articles, emails and social media. Interested biologists, birders, and landowners reported some nests or territories. Extensive surveys on vehicle were conducted for active nests of African woolly-necked storks in potential home range during nesting seasons of 2015 to 2017 concentrating on August and December months when nestlings are present. The African woolly-necked stork builds large nests and they were

easy to sight from roads while travelling in the study areas during the breeding period (pers. obs.).

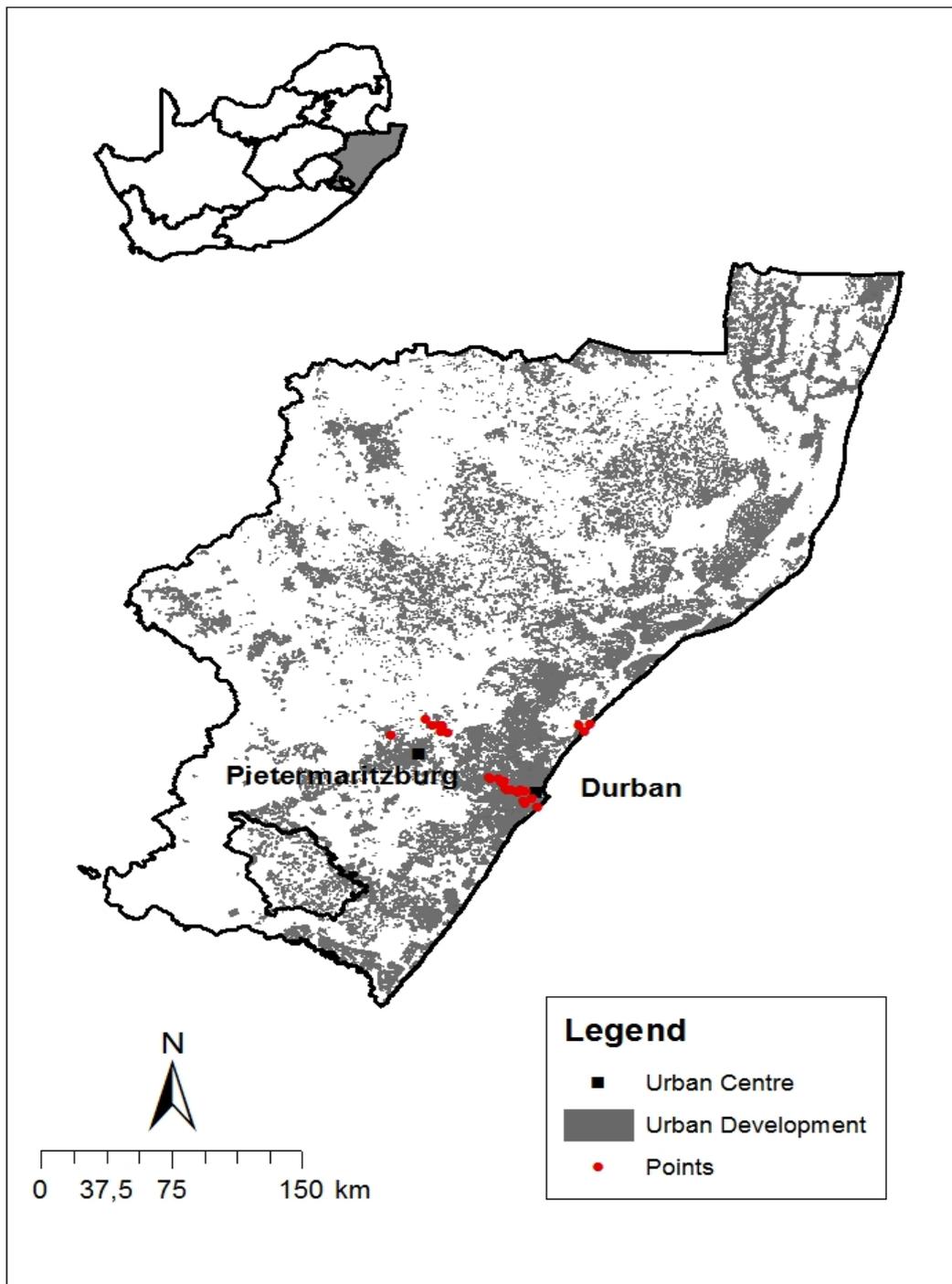


Fig. 4.1 Location of African woolly-necked stork nest sites in suburban areas of KwaZulu-Natal Province, South Africa

Once found, we recorded nest position with a Geographical Positioning System (GPS; Garmin International, Kansas, USA); accuracy: 3–5 m). The nesting tree was identified to species level and tree status (native or exotic) was recorded. We measured nesting tree height with a range finder (Vertex III v.1.5, USA) and diameter at breast height (dbh) with a measuring tape. Other variables pertaining to the nest site characteristics were also measured (Table 4.1).

ArcGIS 10.4 (ESRI, Redlands, USA) was used to compile variables that are known or predicted to influence nest selection and nesting success of the African woolly-necked storks. Microhabitats measurements included the nest distance to the nearest waterbody, nearest building, nearest recreation centre, nearest protected area, and nearest road (Table 4.1).

Table 4.1. Variables used to characterise nest sites of the African woolly-necked storks compared with random sites in this study

Code	Description
microvariables	
trsp	Tree species
height	Tree height (m)
dbh	Nest tree diameter (dbh) (cm)
ten	Tree exotic or native
cott	Condition of the tree (Dead or alive)
nhid/exp	Nest hidden or exposed
macrovariables	
dwetland	distance to nearest wetland (m)
driver	distance to nearest major river (m)
dwater	distance to the nearest artificial waterbody (swimming pool) (m)
dnroad	distance to nearest provincial road (m)
dbuild	distance to the nearest building
dconservancy	distance to the nearest conservancy
recreation	golf courses and managed parks

To examine the differences between nest trees and trees available to African woolly-necked storks, we selected 30 random locations in our study areas by generating random

computer-generated coordinates and transcribing them onto a topographical map. The tree closest to each random point was then located and variables similar to those taken for actual nests were measured. Random sites were at least 2.5 km from any known nest site (mean distance between neighbouring African woolly-necked stork nests (Thabethe and Downs unpublished data)). We considered all random trees to be available to African woolly-necked storks. Some actual nest sites and random sites were on private property to which we did not have access. At these sites, we viewed from a distance, and estimated variables from the distance (average 10 m).

Data analyses

To determine whether African woolly-necked storks select nest sites on the basis of habitat characteristics, we conducted univariate comparisons to test significant differences in microhabitat structure between nest- and random sites. Normally distributed variables were analyzed using independent-sample *t*-tests, but those not meeting normality assumptions after transformation were analyzed using the Mann-Whitney tests. We ran a Chi-square test to determine if there were significant differences between tree species selected for nesting and random sites. Microvariables were tested for normality using a one-sample Kolmogorov-Smirnov test and variables were square root-transformed as appropriate.

Logistic regression, through Generalised Linear Model (GLM) was performed to determine which habitat variables were important in nest-site selection and to identify the set of variables that best separated nest sites from random sites. A logistic regression analysis investigates relations between binary-response probabilities (nest site and random site) and explanatory variables. For GLM, microvariables were not tested for normality as this is not a requirement of logistic regression. We evaluated the data for correlations between variables because highly correlated variables likely measured the same or similar site features. Variables

were only included in the models if correlation among variables was low ($r < 0.70$) to reduce any influence of multicollinearity. Distance to street was excluded because of high collinearity with distance to swimming pool. We used Akaike's information criterion (AIC; Burnham, & Anderson, 2002) to rank models and evaluate support for competing models. We considered the model with the lowest AIC score to be the best model, and we used the difference in AIC values between the best model and the other models in the candidate set to assign model rank (ΔAIC). We considered models with a ΔAIC score of less than 2.0 to be competitive. We determined the weight of evidence for each model using Akaike model weights (w_i), defined as the relative likelihood of a model given all of the models in the candidate set. All data were analysed using SYSTAT and SPSS (SPSS Inc., Chicago, IL, USA) and differences were considered significant at $\alpha < 0.05$.

4.4 Results

We located 30 African woolly-necked storks in KZN between 2015 and 2017 (Fig. 4.1). Most trees were located in front- or backyards of a single-family house in private residences (90.3%) and a few were located in recreational; areas (3.3%), cemeteries (3.3%) and open areas (3.3%) (Table 4.2). There were more nests than expected in the site of high intensity human development and fewer than expected in the site of low intense urban development (Table 4.2). Twenty-seven nests were in trees (90%) while three nests were located on anthropogenic structures (10%). One of these was on the rooftop of a two-story occupied private residence while one was in a special nest box in a tree in a private garden. The other was built on an electric pole. Of the 27 nests located on trees, 23 (85%) were exotic while only four (15%) were native (Table 4.3). African woolly-necked storks built nests in several tree species (Table 4.3), the difference between the sample of trees used and randomly selected sites being statistically significant ($\chi^2 = 99$, $df = 10$, $P < 0.005$). We identified eight different nesting trees

used by African woolly-necked storks (Table 4.3). Most of the nesting trees used by African woolly-necked storks were exotic pine trees (*Pinus elliottii*) followed by eucalyptus trees (*Eucalyptus spp.*) (Table 4.3). African woolly-necked storks were more likely to nest in taller and mature trees. Nest trees were taller ($t = 6.87$, $df = 58$, $P < 0.005$) and greater diameter than random trees ($t = 8.18$, $df = 58$, $P < 0.005$). Trees with nests were 20 - 35 m tall (27.32 ± 5.17 m, mean and standard deviation (SD)) while random trees were 10 - 30 m tall (18.00 ± 5.33 m, mean and SD). For nesting trees, dbh averaged 46.25 cm and ranged from 30 - 80 cm. Nests were generally located on the second branch from the bottom (lower position relative to the canopy height) of the tree, i.e. not in the canopy. All nests were located close to the edge of the branch as far as possible from the main trunk. Nests had clear access to at least one side of the tree and were in close proximity to tall or exposed perches such as power lines. Furthermore, all nests were on live trees.

Table 4.2. Nest sites of breeding African woolly-necked storks in suburban areas of KZN, South Africa in 2015-2017

Location	Number of nests (n)	%
Residential yard	27	90.3
Recreation centre	1	3.2
Cemetery	1	3.2
Natural open area	1	3.2
Total	30	100

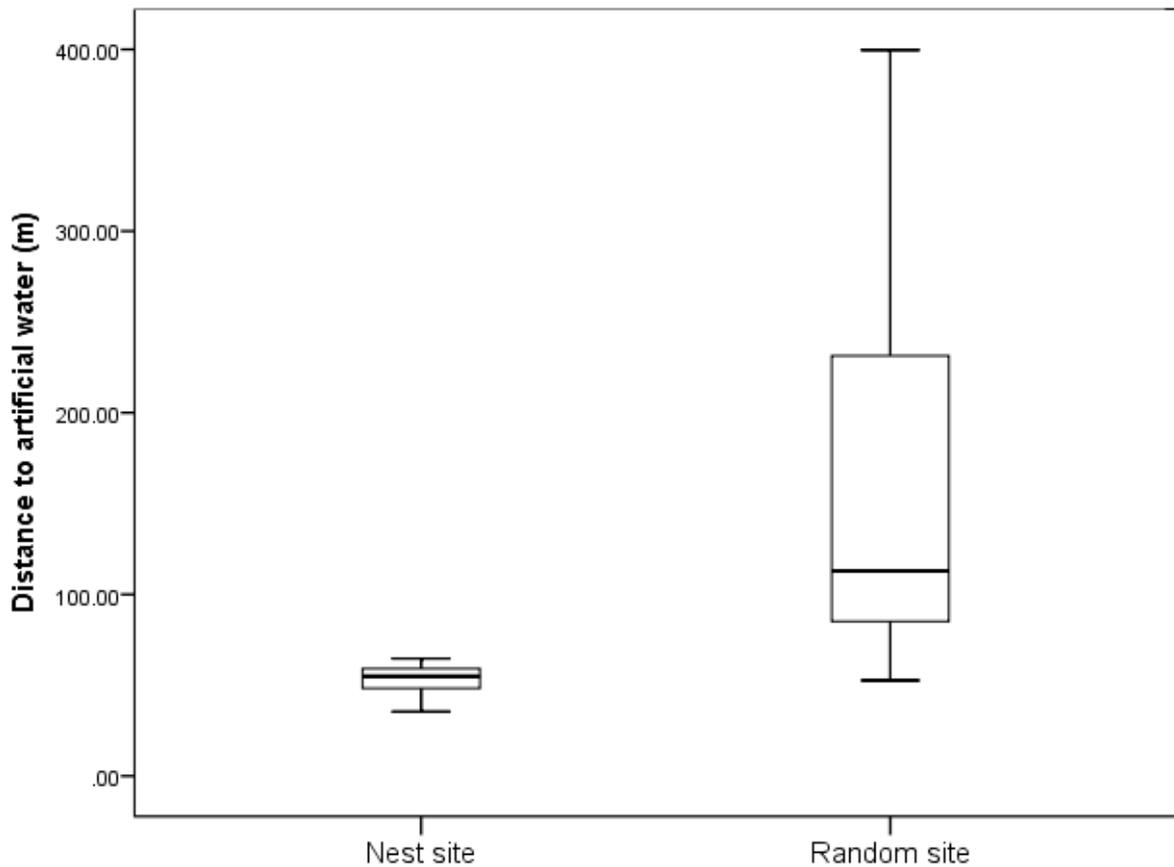


Fig. 4.2 Distance to artificial water (swimming pools) at nests ($n = 30$) and random sites ($n = 30$) of African woolly-necked storks (the bold lines, boxes, and whiskers indicate the median, quartile deviation, and range, respectively)

We compared habitat characteristics at 30 African woolly-necked stork nest sites found in suburban areas of KZN to 30 random sites. African woolly-necked stork nest sites differed from randomly selected sites in several ways. The logistic regression model that best differentiated between nest sites and random sites by considering distance from the nest or random site to nearest artificial water source (swimming pool) and occupied building (single-

family resident) (Fig. 4.3; Table 4.4); had an Akaike weight of 0.16 (Table 4.3). African woolly-necked stork nests were located significantly closer to water (Fig. 4.3) than random points. Two other models were competitive (ΔAIC less than 2) and similar to the best model but also include distance to road and distance to natural wetland respectively (Table 4.4). All other habitat variables received little support in estimating nest site selection (Table 4.4). Although distance from nest or random tree to the nearest recreation centre was not in our logistic regression model, our univariate analyses showed that African woolly-necked storks nest sites were closer to recreation centres than random sites.

Table 4.3. Tree species used as nesting sites by breeding African woolly-necked storks in suburban areas of KZN, South Africa in 2015-2017

Tree species	Number of nests	Exotic or native
<i>Pinus elliottii</i>	12	Exotic
<i>Eucalyptus spp.</i>	6	Exotic
<i>Melia azedarach</i>	1	Exotic
<i>Cinnamomum camphora</i>	2	Exotic
<i>Jacaranda mimosifolia</i>	2	Exotic
<i>Trichilia dregeana</i>	1	Native
<i>Ficus burkei</i>	2	Native
<i>Syderoxylon inerme</i>	1	Native

Table 4.4. Model selection results for logistic regression models for the probability that the site was used for nesting by African woolly-necked stork in suburban

MODEL	Delta			Model	N.Par	LL
	AIC	AIC	Akeike weight	likelihood(LL)		
dbuild+dpool	41.94	0	0.27	1	3	-17.97
dbuild+droad+dpool	43.28	1.34	0.14	0.51	4	-17.63
dwetland+dbuild+dpool	43.62	1.68	0.12	0.43	4	-17.81
dpool	44.78	2.84	0.07	0.24	2	-44.77
dbuild+droad+dprotected+dpool	44.99	3.05	0.06	0.22	5	-17.49
dwetland+dbuild+droad+dpool	45.07	3.13	0.06	0.21	5	-17.53
dprotected+dpool	45.79	3.85	0.04	0.15	3	-19.89
driver+dpool	45.91	3.97	0.04	0.14	3	-19.95
dwetland+dpool	46.44	4.50	0.03	0.11	3	-20.21
droad+dpool	46.44	4.50	0.03	0.11	3	-20.21
dpool+drecreation	46.46	4.52	0.03	0.10	3	-20.23
dbuild+droad+dprotected+driver+dpool	46.71	4.77	0.02	0.09	6	-17.35
dwetland+dbuild+droad+dprotected+dpool	46.83	4.89	0.02	0.09	6	-17.41
dprotected+driver+dpool	47.46	5.52	0.02	0.06	4	-19.72
droad+dprotected+dpool	47.79	5.85	0.01	0.05	4	-19.89
driver+dpool+drecreation	47.86	5.92	0.01	0.05	4	-19.92
dwetland+dbuild+droad+dprotected+driver+pool	48.68	6.74	0.01	0.03	7	-17.34
dbuild+droad+dprotected+driver+pool+drecreation	48.71	6.77	0.01	0.03	7	17.35
droad+dprotected+driver+dpool	49.39	7.45	0.01	0.02	5	-19.69
dprotected+driver+dpool+drecreation	49.40	7.46	0.01	0.02	5	-19.69
dwetland+dbuild+droad+dprotected+driver+pool+drecreation	50.68	8.74	0.00	0.01	8	-17.33
droad+dprotected+driver+dpool+recreation	51.31	9.37	0.00	0.01	6	-19.65
dbuild	59.61	17.67	0.00	0.00	2	-27.80
dbuild+droad	60.99	19.05	0.00	0.00	3	-27.49
dwetland+dbuild	61.14	19.20	0.00	0.00	3	-27.56

dbuild+dprotected	61.32	19.38	0.00	0.00	3	-27.65
dbuild+driver	61.40	19.46	0.00	0.00	3	-27.69
dbuild+drecreation	61.6	19.66	0.00	0.00	3	-27.8
dbuild+droad+dprotected	62.32	20.38	0.00	0.00	4	-27.16
dwetland+dbuild+droad	62.54	20.60	0.00	0.00	4	-27.26
dwetland+dbuild+dprotected	62.77	20.83	0.00	0.00	4	-27.38
dbuild+droad+driver	62.98	21.04	0.00	0.00	4	-27.48
dbuild+droad+drecreation	62.99	21.05	0.00	0.00	4	-27.49
dwetland+dbuild+driver	63.07	21.13	0.00	0.00	4	-27.53
dwetland+dbuild+drecreation	63.14	21.20	0.00	0.00	4	-27.50
dwetland+dbuild+droad+dprotected	63.75	21.81	0.00	0.00	5	-26.87
dbuild+droad+dprotected+drecreation	64.12	22.18	0.00	0.00	5	-27.16
dbuild+droad+dprotected+driver	64.29	22.35	0.00	0.00	5	-27.14
dwetland+dbuild+droad+driver	64.52	22.58	0.00	0.00	5	-27.25
dwetland+dbuild+droad+drecreation	64.54	22.60	0.00	0.00	5	-27.26
dwetland+dbuild+droad+dprotected+driver	65.74	23.80	0.00	0.00	6	-26.86
dwetland+dbuild+droad+dprotected+drecreation	65.74	23.80	0.00	0.00	6	-26.87
dbuild+droad+dprotected+driver+drecreation	66.29	24.35	0.00	0.00	6	-27.14
dwetland+dbuild+droad+dprotected+driver+drecreation	67.73	25.79	0.00	0.00	7	-26.86
dwetland+dprotected	86.10	44.16	0.00	0.00	3	-44.04
dprotected	86.12	44.18	0.00	0.00	2	-41.01
droad	86.18	44.24	0.00	0.00	2	-41.09
driver	86.97	45.03	0.00	0.00	2	-41.48
drecreation	87.14	45.20	0.00	0.00	2	-41.57
dwetland	87.17	45.23	0.00	0.00	2	-41.58
droad+dprotected	87.63	45.69	0.00	0.00	3	-40.81
dprotected+driver	88.08	46.14	0.00	0.00	3	-41.03
dprotected+drecreation	88.10	46.16	0.00	0.00	3	-41.05
droad+drecreation	88.15	46.21	0.00	0.00	3	-41.07
dwetland+droad	88.18	46.24	0.00	0.00	3	-44.09

droad+driver	88.18	46.24	0.00	0.00	3	-41.08
driver+drecreation	88.93	46.99	0.00	0.00	3	-41.46
dwetland+driver	88.96	47.02	0.00	0.00	3	-41.48
dwetland+drecreation	89.14	47.2	0.00	0.00	3	-41.57
droad+dprotected+drecreation	89.61	47.67	0.00	0.00	4	-40.80
droad+dprocted+driver	89.61	47.67	0.00	0.00	4	-40.80
dprotected+driver+drecreation	90.05	48.11	0.00	0.00	4	-41.02
droad+dprotected+driver+drecreation	91.59	49.65	0.00	0.00	5	-40.79



Fig. 4.3 Example of a typical nest site of African woolly-necked storks in an exotic pine tree in a residential garden in a suburban area of KZN, South Africa

4.5 Discussion

This study provides the first evidence that African woolly-necked storks have successfully established breeding sites in suburban areas in KZN, South Africa. Most nest sites were located in the yards of single-family residences and few were in recreational areas, cemeteries, street trees and natural open areas. The presence of African woolly-necked storks in suburban areas is unexpected and contradictory observation because this species was regarded highly sensitive to human disturbance, especially during the breeding season and considered to only nest in natural wetlands away from human habitation (Clancey 1964; Cyrus and Robson 1980; Allan 2012). There are several factors that are likely to make suburban areas of KZN attractive to African woolly-necked storks. The first factor is the availability of tall trees as urban gardens mature. The growth in urbanisation and development of suburban areas in KZN has resulted in the introduction of trees

to previously treeless areas and these trees are now dominant (Singh and Downs 2016). These suburban areas have established domestic gardens with tall trees, especially exotic ornamentals (Singh and Downs 2016). The present work found that African woolly-necked stork generally selected tall exotic trees especially pine and eucalyptus trees. This might suggest that planting of exotic trees has contributed to the establishment of African woolly-necked stork breeding sites in suburban areas by providing suitable nest trees that were previously unsuitable for breeding. There are several other native birds nesting in relatively tall, exotic, garden trees in our study area including hadeda ibis (*Bostrychia hagedash*) (Singh and Downs 2016) and crowned eagles (*Stephanoaetus coronatus*) (McPherson et al. 2016). Furthermore, throughout the world exotic trees are often used as nest sites by native bird species and are sometimes preferred over native trees (Boal and Mannan 1998).

Though the African woolly-necked stork is known to normally nest mainly in trees, here we report three instances of it nesting on anthropogenic structures including rooftops, nest-boxes and power line poles. There are no prior reported instances of this species nesting on anthropogenic structures. The shift in nesting sites from natural places to anthropogenic structures in suburban environments may reflect the ability of birds to adapt to urban ecosystems (Wang et al. 2008). Such adjustments in nesting behaviours have been reported in other storks including Asian woolly-necked storks (Vaghela et al. 2015), white storks (*Ciconia ciconia*) (Bochenski and Jerzak 2006), black storks (*Ephippiorhynchus asiaticus*) (Gopi, 2003) and marabou storks (*Leptoptilos crumeniferus*) (Pomeroy and Kibuule 2017). Although only few nests were located on anthropogenic structures in this study, the shift from natural structures might have important consequences for the persistence of this species in suburban environments in the future.

In this study, all nest trees were mature, taller and of greater diameter than random sites. This agrees with Cyrus and Robson (1980), who state that African woolly-necked storks generally prefer taller and larger trees in their natural habitats. We assume that African woolly-necked storks select taller trees most probably for security and protection of nestlings from any disturbance within close proximity to the nest. However, we doubt that level of human disturbance influenced the selection of nest sites because most nests were located in occupied family yards and three nests overhung two-lane suburban roads with almost constant human disturbance from both pedestrians and cars. Furthermore, nest sites were located closer to roads than random points which suggests a high tolerance to human activity and emphasises a close association with human settlements. It is most likely that African woolly-necked storks select nests closer to roads because they are attracted to the taller, street trees that often line busy roads not because of high human disturbance per se. Tree species that were mostly used for nesting had fewer and thicker side branches. This potentially offered adequate support to the voluminous platform nest of the African woolly-necked storks. All nests were built on flat horizontal side branches away from the main trunk. The reason to place nest at the tip of branches as opposed to the fork might be to avoid climbing nest predators from entering the nest.

The second factor potentially making suburban areas attractive to breeding African woolly-necked storks was availability of water. Most residential homes had a swimming pool in our study areas (pers. obs.). Unsurprisingly, our study revealed that African woolly-necked stork nest sites were significantly closer to water (swimming pools) than random sites. As expected, water was a main factor in determining the nest site selection in African woolly-necked storks. The additional accessibility of water at the numerous bird-baths, artificial ponds, roadside puddles and irrigated mowed lawns in these suburban areas may further favour suburban nesting by African woolly-

necked storks. Although previously associated with natural wetlands, African woolly-necked storks in suburban areas were not significantly closer to natural water sources than random sites. This can be explained by these artificial water sources providing accessible drinking water and suitable foraging habitats. The proximity of African woolly-necked stork nests to water may, therefore, be adaptive in terms of optimising foraging activities.

Availability of food was the third reason likely making suburban areas of KZN attractive to African woolly-necked storks. Suburban areas generally offer more abundant and constant food for many bird species worldwide (Gilbert et al. 2016). Supplementary feeding of African woolly-necked storks is common and widespread among suburban areas of KZN (where all nests are situated) with several people feeding on a daily basis and year-round (Thabethe and Downs 2018). Birds are known to locate their nesting sites within the foraging site so as to reduce the number of trips to the nest. The fact that all nests were located in close proximity to occupied family buildings again reiterates the point that nesting African woolly-necked storks probably select nest sites near feeding sites. African woolly-necked storks also naturally forage on watered lawns, in recreational areas (mostly golf courses) and in landfill sites around our study area (Berruti 1997; Thabethe and Downs 2018). The high availability of food in close proximity to nest sites suggests that African woolly-necked storks need not travel far to look for food and therefore might have small home ranges. The abundance of stable supplementary and available foraging opportunities from lawns may explain the high nesting density of African woolly-necked storks in these suburban areas. The abundance of sufficient food in suburban areas might be the reason why we did not find nest sites established in natural habitats despite the abundance of natural wetlands (including rivers, dams and lagoons) in KZN.

African woolly-necked storks are not the first stork species that has established breeding sites in urbanised habitat. Several species in the family Ciconiidae are successfully breeding in urban areas across the world including the white stork in Europe (Onmus et al. 2012), marabou stork in Africa (Pomeroy and Kibuule 2017), the Asian woolly-necked stork, black stork (Gopi 2003) and Asian openbill stork (*Anastomus oscitans*) in India (Anila et al. 2016).

This study showed a positive impact of urbanisation on once endangered species (del Hoyo et al. 2018) and a possible role that humans can play in this regard through adequate management of suburban areas. The increase in African woolly-necked stork populations in South Africa during recent decades (Berruti 1997; SABAP 2018) may be a consequence of the species' capacity to adapt to environmental change and human disturbance. Contrary to expectations, this study showed that African woolly-necked storks are not a typical wetland species. This could be an example of rapid adaptability of wildlife to anthropogenic developments. For successful long-term conservation of African woolly-necked storks, it is crucial that the existing nesting trees are protected with no or minimal alteration to the surrounding habitat. Of concern, the majority of African woolly-necked stork bred in privately owned nesting trees or rooftops, therefore their future might depend on the willingness and support of the landowners. We therefore propose that all households should be asked to conserve active nest trees. Furthermore, exotic tall trees especially pine and eucalyptus trees should be conserved in suburban areas of KZN. This might be controversial since these trees are invasive in South Africa, however the removal or eventual death of existing nest trees, could decrease suitable nest sites for African woolly-necked storks in these suburban landscapes.

Future studies should investigate food requirements at nest sites and post-fledging survival must be accessed to determine their nesting success. To our knowledge, this is the first study

reporting African woolly-necked breeding in suburban areas and determining the factors influencing nest sites selection in these areas, which thus fills in a significant gap. Future work should examine food requirements at nest sites and post-fledging survival to determine nesting success and whether this population is acting as a source or a sink.

4.6 Acknowledgements

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CHAPTER 5

Nestling provision and breeding behaviours of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa

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Running header: Nestling provision and breeding behaviours of African woolly-necked storks

5.1 Abstract

African woolly-necked storks (*Ciconia microscelis*) have recently colonised many suburban areas in KwaZulu-Natal, South Africa, but data on breeding and foraging behaviour of these populations are lacking. We therefore, investigated nestling provision and breeding behaviour of African woolly-necked storks in ten nests using direct observations and infrared camera traps during three breeding seasons (2015-2017). Time-lapse cameras were positioned at urban nest sites (n = 6) to identify the prey composition during 2017 breeding period (August - December). African woolly-necked storks consistently reoccupied the majority of nest sites across study years since initial discovery, suggesting that this population was at least stable. We documented evidence of cooperative breeding where by more than two adults provided care to a single nest. Three nests were found in which at least three adults provisioned or guarded the nestlings in this study. This is the first-time cooperative breeding has been reported in the African woolly-necked stork – a

novel behavior for this species. Evidence of cooperative breeding may mean that this species has a flexible social structure, allowing it to employ different breeding tactics in different environments. Both parents and helpers participated in the provisioning of nestlings throughout the day, making an average of 9.7 daily visits with food. African woolly-necked storks provisioned their nestlings predominantly with natural food, primarily amphibians particularly guttural toads (*Amietophrynus gutturalis*). However, African woolly-necked storks did provision their chicks with anthropogenic food including polony, sausages and cooked chicken. Preferential provision of natural food to nestlings may be due to the need of adequate amount of protein content and high-quality food for nestlings. The diet composition indicated that African woolly-necked storks foraged mainly in domestic gardens during the breeding season. Our result demonstrates the adaptive foraging ability of African woolly-necked storks in urban areas which is important for ensuring sufficient provisioning of nestlings. The variation in diet and opportunistic use of locally abundant prey within suburban areas underscores the plasticity of African woolly-necked feeding behaviour. This plasticity may in part explain this African woolly-necked stork's ability to occupy a wide variety of habitats in KwaZulu-Natal.

Key words: African woolly-necked storks, anthropogenic food, breeding behaviour, cooperative breeding, nestling provision

5.2 Introduction

As urban development expands to meet the demands of a growing human population, natural habitats and species compositions are changing dramatically (Seto et al. 2012, Aronson et al. 2014, Seress and Liker 2015). Urban expansion is known to threaten biodiversity as a result of habitat loss or fragmentation (Cohen 2006, Seress and Liker 2015). Despite this, an increasing number of species occupies urban areas (Blanco 1997, Marzluff and Ewing 2001, Shochat et al. 2010, Calle and Gawlik 2011). Occupancy of birds in urbanised environments depends on the capacity of urban habitats to provide sufficient nest sites, roosts, and food resources (Marzluff 2001, Moller 2009, Galbraith et al. 2014, Cereghetti 2017, Jagiello et al. 2018). Most importantly, the ability to successfully utilise these resources is the key to the survival of urban bird species (Ditchkoff et al. 2006, Henderson 2015). Consequently, urbanisation is associated with acquisition of new behaviours or with behavioral shifts (Ditchkoff et al. 2006, Robb et al. 2008, Gillanders et al. 2017). Changes in the diet of birds have been observed and described in urban environments throughout the world (Heiss et al. 2009, Johnson et al. 2010, Hilgartner et al. 2014, Gilbert et al. 2016). The diet change often includes utilisation of various kinds of anthropogenic food such as direct supplementary feeding and food from landfills (O’Leary and Jones 2006, Kruszyk and Ciach 2010, Calle and Gawlik 2011, Ezaki and Ohsako 2012, Gillanders et al. 2017). Irrigated parks and landscaped gardens also provide reliable and predictable sources of natural food for urban birds (Krystofkova et al. 2011, Cava and Stewart, Leveau and Leveau 2016).

High abundance of anthropogenic food associated with urban areas can aid in the establishment of a viable, self-sustaining population by increasing growth rates, survival and social interactions rate (Lowry et al. 2012). However, anthropogenic food may cause negative effects to some birds especially nestlings, which may subsequently reduce reproductive success (Meyrier et

al. 2017). As such, it has been reported that several urban bird species mainly provision natural food to nestlings despite the abundance of anthropogenic food in urban areas (Blanco 1997, O'Leary & Jones 2006).

Nesting behavioural adaptations are significant as crucial determinants for successful establishment and persistence of birds in urbanised landscape. Sometimes the behaviors identified in urban individuals are innovative in that the behavior is being observed or recorded for the first time (Kark et al. 2007). Several bird species have showed behavioral shifts to persist in urban areas. black storks (*Ciconia nigra*) and white storks (*Ciconia ciconia*) (Tortosa et al. 2002, Hilgartner et al. 2014, Jagiello et al. 2018).

African woolly-necked stork populations in KwaZulu-Natal Province, South Africa have increased considerably and, despite their previous known avoidance of humans, these storks have begun invading suburban in large numbers (Birdlife International 2018, del Hoyo et al. 2018, SABAP2 2018). However, there is no information available on breeding behavior and nestling provision in this population. The available information regarding the breeding behaviour of the African woolly-necked stork is based on anecdotal information. Here we documented the breeding behavior and nestling provision of the African woolly-necked storks over three breeding seasons in suburban areas of KwaZulu-Natal, South Africa. Recently it was confirmed that the African woolly-necked stork is an opportunistic species that feeds on supplementary anthropogenic food on a daily basis throughout the year (Thabethe and Downs 2018), although its natural diet is entirely carnivorous including insects, amphibians and other small vertebrates (del Hoyo et al. 2018). It was therefore predicted that the diet of nestlings would comprise primarily of anthropogenic food as many people are feeding African woolly-necked storks in suburban areas of KwaZulu-Natal.

5.3 Methods

Study area

This study was conducted in KwaZulu-Natal, South Africa (Chapter 4). The subtropical climate of KwaZulu-Natal makes the province ideal for a number of wildlife (McPherson et al. 2016). The African woolly-necked stork has established a breeding population in suburban areas of KwaZulu-Natal (SABAP2 2018; Thabethe and Downs unpublished data). KwaZulu-Natal has the largest population of African woolly-necked storks associated with urban landscapes in South Africa (Allan 2012, SABAP2 2018).

Nests

During 2016 to 2017 there were 30 African woolly-necked stork nests located in suburban areas of KwaZulu-Natal Province, South Africa (Chapter 3). From these nests, ten nests were selected to study the breeding biology of African woolly-necked storks. All nests were located in yards of single-family residences. We recorded nesting behaviour, feeding behaviour and food brought to the nestlings by adult African woolly-necked storks during three breeding seasons using direct observations and camera-traps (Ltl Acorn 5210MG and 6210MG, with rechargeable AA batteries and 32 GB SDHC memory card). During the 2015 and 2016 breeding seasons, we collected data on the behaviour of ten active African woolly-necked storks adults/parents using direct observations every week from incubation to hatching. During a 30-min. observation period, the total number of nest visits by each parent bird and the type of prey delivered to the nestlings was recorded using binoculars. However, during the 2017 breeding period activities at the nests were obtained using six camera-traps. These were installed from 2 - 3.5 m from the front edge of each

African woolly-necked stork nest, between 20- and 80-degrees pitch. The camera-traps were installed when the African woolly-necked stork chicks were about 20 - 30 days old on warm shaded days. All camera-traps were removed after fledging and the chicks fledged around 60 days. Nests were between 10 and 25 m above ground and accessed using a fixed-rope jumar technique. This technique posed no hazard to either the adults or young and allowed for the near continuous monitoring of nest behaviour for both nestling and adults (Franzreb and Hanula 1995). All field activities were performed with an Ezemvelo KZN Wildlife permit and the University of KwaZulu-Natal Animal Ethics approval.

Five camera-traps were set to operate only in diurnal periods (30 min. before sunrise to 30 min. after sunset), while one camera-trap was set to operate for 24 h. A time lapse schedule of 1 image /1 min was employed until the chicks fledged throughout the duration of the study. African woolly-necked stork camera-trap data were reviewed in continuous sequences and prey items were tracked from arrival to consumption and/or discard. Food items were identified from photographs; if the food could not be reliably identified, it was noted as undetermined. Images were catalogued to a food items table. Furthermore, images obtained from the camera-traps were scanned for any event (where an event was defined as a picture that had predators or competitors and other social behaviour). The feeding frequency of chicks (number of feedings per day) was measured from sunrise to sunset in 2017 breeding period. We recorded the total number of nest visits by each adult, the frequency of prey deliveries and the total duration that each adult spent at the nest. The types of food delivered to the nestlings were recorded.

5.4 Results

Nestling provision

The diet of African woolly-necked stork nestlings included natural (wild prey) and anthropogenic food (Fig. 5.1). The amount of natural food (69%) provided nestlings was higher than that of anthropogenic food (31%) (Fig. 5.1). The guttural toad (*Amietophrynus gutturalis*) was the most important prey in the diet of African woolly-necked stork nestlings (63%) (Table 5.1). The common river frog (*Amietia quecketti*) was also provisioned to the nestlings. Fish, snakes, crabs and mammals were rarely recorded (Table 5.2). Most of the anthropogenic food was small pieces of processed meat such as polony, sausages and cooked chicken. The composition of the nestling diets was similar for all age-classes. Food was delivered throughout breeding season. The mean feeding rate for six African woolly-necked stork nests was 9.7 provisioning visits per day (Fig. 5.2). There was no linear relationship between the age of the nestlings and the feeding rate (Fig. 5.2). The peaks of food provisioning during the day were between 07h30 – 08h30 and 17h00 – 18h00.

Table 5.1. The diet of African woolly-necked stork in suburban areas of KwaZulu-Natal, South Africa. Diet was assessed using time-lapse cameras at six nests sites

Species	Common name	Number of items	%
<i>Amietophrynus gutturalis</i>	Gutteral toad	387	63.9
<i>Amietia quecketti</i>	Common River Frog	16	2.6
<i>Hyperolius marmoratus</i>	Painted Reed Frog	6	0.9
<i>Philothamnus semivariiegatus</i>	Spotted bush snake	3	0.5
<i>Chrysochloris asiatica</i>	Golden mole	2	0.3

Fish	2	0.3
Crabs	1	0.2
Anthropogenic food	186	30.7
Total	606	100

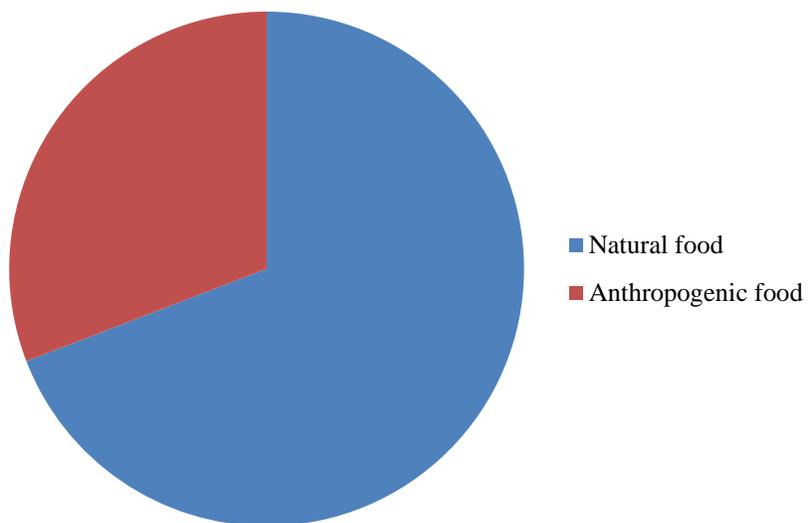


Fig. 5.1 Number of items of natural and anthropogenic foods provisioned to chicks by African woolly-necked stork adults at six nests in the present study.

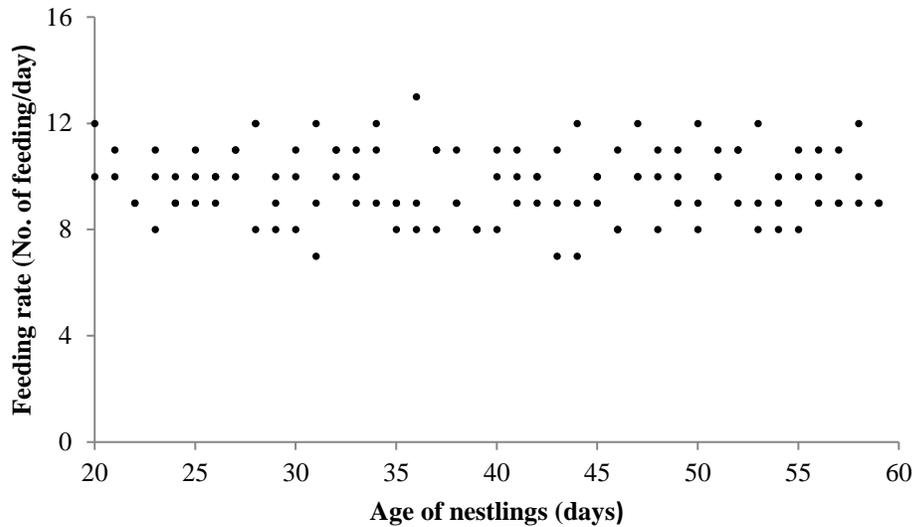


Fig. 5.2 Feeding frequency (number of feeding events/day) at six African woolly-necked stork nests

Breeding biology

The African woolly-necked storks breeding season generally ran from August to December, with the exception of two breeding attempts in March and April of which both were unsuccessful. The nest building started in early August and both male and female built the nests. Once the nest was completed, courtship continued. The courtship display involved making bill-clatters at the nest, with the head resting back on the upper back of the other bird (Fig. 5.3a). Several days after the initial copulations (Fig. 5.3b), the female began to lay a total of two to four creamy white eggs (Fig. 5.3c). The incubation period lasted about 28 - 30 days and was shared by both parents. The eggs were never left unattended; each parent spent a mean of 3 h incubating at a time. After sitting for several hours, the brooding bird sometimes stood up, stretched, preened, flapped, rearranged nest sticks, pulled twigs from branches around the nest, or turned the eggs with its bill before

sitting again. Green leaves were brought into the nest throughout the breeding period. The African woolly-necked storks hatched asynchronously; therefore, the nestlings were of different sizes (Fig. 5.3d). The newly-hatched storks remained without feathers for the first few days (Fig. 3d). Within several days, however, the feathers started to develop until fully developed (Fig. 5.3f). During the first few days of hatching the young lay quietly in the nest except during feeding and become more active after two weeks. After a month the young were more alert (Fig. 5.3f). The chicks fledged 60-65 days after hatching. African woolly-necked storks fed their young by regurgitating food items onto the nest platform, where the young picked up the items and fed. The African woolly-necked stork is monomorphic, so we could not identify the sex of individuals.





Fig. 5.3 Nesting behaviour, eggs and nestlings of African woolly-necked storks showing (A) Courtship, (B) copulation, (C) creamy white eggs, (D) nestlings with grey feathers, (E) nestlings with developing woolly-necked stork, and (F) fully developed nestlings

Nests re-use

In this study all African woolly-necked storks nest sites were re-used over each year in three consecutive breeding seasons. New nests were built in the same tree and usually on the same branch in the event when the actual nest was destroyed by the following breeding season. The African woolly-necked storks were not marked therefore it was not possible to know whether the same pair re-used the nests in the following season. In the first two breeding seasons all nests were successful. In 2017 breeding period, eight of ten nests were successfully in their breeding attempt with nestlings that fledged while two nests were not successful.

Nest competition and other species at the nest

In the 2017 breeding period, two African woolly-necked stork nests were preyed on by Egyptian geese (*Alopochen aegyptiaca*) (Fig. 5.4). These geese destroyed the eggs, took over the nests and

bred successfully in both instances. Purple crested turaco (*Gallirex porphyreolophus*) was the only frugivorous bird species recorded at one nests of the African woolly-necked stork.



Fig. 5.4 A lone Egyptian geese at the nest of the African woolly-necked stork in the present study



Fig. 5.5 Evidence of cooperative breeding in African woolly-necked storks where (A) is two nestlings with two adults (normal behaviour), (B) three adults at the nest with two nestlings during the day, and (C) three adults with two nestlings at night

Evidence of cooperative breeding

Of the ten African woolly-necked storks nests monitored, we recorded evidence of cooperative breeding in three nests. Camera-traps revealed an additional adult at three nests on regular basis during the breeding period (Fig. 5.5 a, b, c). Helpers were observed both during the day (Fig. 5.5 b) and at night (Fig. 5.5 c). Helpers did not contribute to nest construction, incubation nor brooding, but were only involved in feeding of nestlings.

5.5 Discussion

Nestling provision

African woolly-necked storks provisioned their nestlings with both natural and anthropogenic food in suburban areas of KwaZulu-Natal, South Africa during the breeding season. However, amphibians, particularly guttural toads were the main prey of the African woolly-necked stork nestlings. African woolly-necked storks are known to feed on amphibians in their natural range (del Hoyo et al. 2018). These findings have two potentially important implications. Firstly, the guttural toads might have a larger population relative to other frog species therefore be readily available for storks in KwaZulu-Natal. Indeed, an article by Evans (2015) suggests that guttural toad is one of the most common frogs, which is infamous for taking up residence in suburban gardens across our study area. It is worth to note that the guttural toad is domestic invasive in some parts of South Africa (e.g. Cape Town) (Vimercati 2017). Secondly, the consistently high frequency of guttural toads we recorded in the diet across all six nests provided evidence that African woolly-necked storks opportunistically use locally abundant prey within suburban areas, emphasising the plasticity of the species. Falk et al. (2006) found that amphibians are the key prey for Abdim's storks (*Ciconia abdimii*) in Niger. Furthermore, Kopij (2003) recorded a large

proportion of frogs (*Pyxicephalus adspersus*) in cattle egret nestling diet in South Africa. Natural food including fish, crabs, reptiles and golden moles were also provisioned to nestlings of the African woolly-necked storks in this study. All-natural prey species recorded occurred in domestic widely gardens within the study area. The diet composition indicated that African woolly-necked storks foraged mainly in gardens during the breeding season.

African woolly-necked storks also fed anthropogenic food to their nestlings including polony and sausages, further confirming that this species can exploit human landscapes. Although anthropogenic food was provisioned to African woolly-necked storks, natural food was the major food fed to nestlings in our study. Our results suggest that natural food was a more important food resource for breeding African woolly-necked storks. This is despite a significant number of householders feeding African woolly-necked storks daily throughout the year in KwaZulu-Natal (Thabethe and Downs 2018). Previous studies have indicated that urban birds may be selective in what they provide their nestlings (Alley, 1979). Blanco (1997) found that black kites (*Milvus migrans*) consumed mainly anthropogenic food during the non-breeding season and shifted towards a more natural diet when breeding. Furthermore, O'Leary and Jones (2006) found that Australian Magpies (*Gymnorhina tibicen*) were not reliant or dependent on supplementary food provided by wildlife feeders. Although many Australian magpies did utilise suburban feeding stations extensively, they continued to forage for and provision their chicks with natural food especially insects. Preferential provision of natural food to nestlings may be due to the need of adequate amount of proteins and high-quality food. Indeed, Heiss, et al. (2009) reported that anthropogenic food had a low protein content to replace natural food resources, especially for chick rearing. Therefore, high amount of anthropogenic food in the diet may lead to dietary deficiencies and could negatively affect the growth of the nestlings.

The effect of consuming significant amounts of supplementary food is largely unknown for the African woolly-necked storks, however a recent local article by Chittenden (2018) reported that two chicks of the African woolly-necked storks died and assumed to have succumbed from anthropogenic processed food (polony) almost on daily basis at their nest site in KwaZulu-Natal. Chittenden (2018) reported that chicks had slow growth presumably from an unhealthy diet. This is of great concern and it is therefore highly advisable that processed meat is not fed to African woolly-necked storks, especially during breeding, as it may have lethal effects on nestlings: alternatively, raw meat such as chicken may be fed.

There are conflicting reports on the effects of anthropogenic food on the nesting success of breeding birds. A study of white stork populations in Spain showed that birds using anthropogenic resources during the breeding season had higher nesting success than did those birds at control sites (Tortosa et al. 2002). In contrast, Rumbold et al. (2009) found that a mixed colony of wading birds that foraged at a landfill had reproductive rates similar to those of other colonies in the region. Exactly how differences of nutrition between anthropogenic and natural food may affect African woolly-necked stork growth and survival will require additional research. The fact that many domestic households have been feeding for several years (Thabethe and Downs 2018) suggests that a long-term effect of this activity might already be acting on the African woolly-necked storks in the area. Given the increasing presence of African woolly-necked storks in KwaZulu-Natal, negative effects that would normally reduce population size significantly (e.g. higher mortality) are low.

We did not find any relationship between nestling age and feeding rate and feeding frequency found in our study was similar for all nests. Similarly, Steiner and Spaari (2001) described that food-provisioning frequencies of white stork chicks did not change significantly

with nestling age or time of the day. Furthermore, Hampl et al. (2005) reported that black stork feeding frequency did not differ with nestling age. No data on African woolly-necked storks feeding frequency have been published elsewhere to compare. We had no means to assess if the food brought to the chicks differs from the diet of the adults during breeding season.

Breeding biology

The current study has demonstrated that African woolly-necked storks breed both regularly and in large numbers suburban areas of KwaZulu-Natal. This is in contrast to the published literature (Cyrus and Robson 1980) that suggests that this stork only bred in natural wetlands way from human disturbance. The fact this population has been breeding regularly for at least the past three years (and probably more than 10 years as reported by the public), suggest that this suburban population is stable and important for the conservation of this species in the region. African woolly-necked storks typically lay 2 – 4 eggs (Sinclair et al. 2011) as was the case in the present study, and where the maximum number of chicks fledged at a single nest was three. Our overall results on the breeding biology of the African woolly-necked storks are consistent with the breeding biology described by Sinclair et al. (2011). However, in two instances storks tried to breed in March and April which was outside their breeding period, this suggests the possibility of extended breeding periods in the suburban populations of African woolly-necked storks.

Nests re-use

This is the first study that provides evidence of African woolly-necked storks nest re-uses over several years in South Africa. It is considered that the same stork pairs re-used the same nest sites year after year in this study, although evidence was hard to obtain since none of the storks were

marked. Nest re-use is common among storks, for instance a pair of banded oriental white storks in Japan reused the same nests over years (Ezaki and Ohsako 2012). Additionally, it was reported recently that a pair of Asian woolly-necked storks re-used the same nest site in India over three breeding seasons (Purbasha 2017, Greeshma et al. 2018). Studies suggest that nest re-use may play an important role in breeding success (Moreno 2012). White storks that re-used nests had higher breeding success than those that built new nests partially due to costs associated with building a new nest (Tobolka et al. 2013).

Nest competition and other birds in the nest

There was competition for nest-sites in suburban areas of KwaZulu-Natal, and the Egyptian goose was the only other species directly competing with the African woolly-necked storks. Although only few incidents of nest usurpation were recorded in this study, Egyptian geese might have significant impacts on African woolly-necked storks in future because their population is increasing rapidly in South Africa. For instance, opportunistic nest usurpation by Egyptian geese appears to be an increasing problem for species such as sparrow hawks in South Africa (*Accipiter melanoleucus*) (Curtis et al. 2007). African woolly-necked storks showed indifference to purple crested turaco that visited the nests. This phenomenon of other bird species visiting stork nests is well known in white storks. For example, white storks usually tolerate sparrows (*Passer spp.*) and European starling *Sturnus vulgaris* in their nest (Bochenski 2005).

Evidence of cooperative breeding

We documented the first evidence of African woolly-necked storks cooperative breeding where more than two adults provided care to a single nest sites in KwaZulu-Natal Province. Three nests

were found in which at least three adults provisioned the nestlings in this study. To date, the observations reported here are the only occasions where more than two individuals were recorded supplying food to nestlings in this traditionally pair-breeding species. The additional adults on the nest may have been nonbreeding young that remain at the natal site and help to care of their own siblings (Koenig 2017). Alternatively, helpers may be unrelated individuals that may produce offspring within the group (Koenig 2017). In this study of the African woolly-necked storks, we could not identify relatedness of the helpers because they were not ringed. We do not believe that habitat saturation (a shortage of territories) caused this occurrence of cooperative breeding, as would be predicted by the ecological-constraints hypothesis. There were enough suitable available nesting sites present in the breeding area since they generally nest in alien pine (*Pinus spp.*) and eucalyptus (*Eucalyptus spp.*) trees and sometimes on anthropogenic structures (Thabethe and Downs, unpublished data). There was no evidence from previous records to suggest cooperative breeding behaviour in African woolly-necked storks historically (Cyrus and Robson 1980). It is appropriate, therefore, to view the cooperative breeding in this species as a novel behaviour that has developed in recent years. These results could help understand understand the evolutionary origins of cooperative behaviour in birds. Further studies involving the marking of nestlings, combined with nest observations to determine group composition and relatedness should be conducted.

Conclusion

Our study revealed that African woolly-necked storks provisioned their nestlings with both natural prey and anthropogenic food in suburban areas of KwaZulu-Natal. The variation in diet and opportunistic use of locally abundant prey within suburban areas highlights the plasticity of

African woolly-necked feeding behaviour. Evidence of cooperative breeding may mean that this species has a flexible social structure, allowing it to employ different breeding tactics in different environments. These behavioural flexibilities may potentially facilitate the species survival and persistence in urbanised environments.

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CHAPTER 6

CONCLUSIONS

6.1 Introduction

Urbanisation is the main driver of land-use changes and a major threat to global biodiversity (Seto et al. 2012, Aronson et al. 2014, Seress and Liker 2015). With the current projections indicating that world population will reach 9.3 billion people by 2050, urbanisation is likely to increase and consequently biodiversity loss is likely to escalate in the near future (Cohen 2006, United Nations 2014). Therefore, understanding how some avian species persist and utilise urbanised environments is critical for their conservation (Lowry et al. 2012). Avian populations within urbanised areas provide unique situations in which to undertake research on how species adapt and survive in novel environments (Gilbert et al. 2016). Birds have been one of the most intensively studied taxa in urban environments. However, most studies have mainly been conducted in the Northern Hemisphere, especially North America and Europe. On the other hand, there are only few studies in other continents such as South America and Africa. This has left the Southern Hemisphere underrepresented within the urban ecological literature. Studies of urban avifauna at these understudied continents are however necessary if we are to obtain a global perspective of urban ecology (Marzluff 2001). As such, this thesis aimed to address this issue and, more specifically, it was aimed at examining several key aspects of the ecology, population dynamics, and breeding behavior of African woolly-necked storks (*Ciconia microscelis*) in suburban areas of KwaZulu-Natal Province, South Africa.

Understanding of a species' occupancy, abundance and distribution is vital for conservation, management and striking the right balance in avoiding human-wildlife conflict. Therefore, using data from a citizen science monitoring program (Coordinated Water bird Counts),

I determined long-term trends (1992-2017) in occupancy, colonisation and extinction of African woolly-necked storks as a function of change in land cover across KwaZulu-Natal. The wetland occupancy of African woolly-necked storks was relatively stable across 27 years. However, this species had rapidly extended their distribution range to urbanised environments over the duration of monitoring, becoming common in KwaZulu-Natal (Chapter 2). African woolly-necked stork populations have taken advantage of recent anthropogenic development, especially man-made wetlands. These results contradict the traditional view that only natural wetlands far away from human disturbance support high colonisation of this bird. African woolly-necked storks, once rare and endangered throughout the region, now have a stable population and common in KwaZulu-Natal.

Supplementary feeding has been highlighted as one of the main factors that enable avian species to persist in urban areas. Through citizen science, we assessed the extent to which householders in urban and suburban areas of KwaZulu-Natal provide supplementary food to African woolly-necked storks (Chapter 3). The majority of respondents fed the African woolly-necked storks on daily basis throughout the year (Chapter 3). This may be a defining factor influencing their persistence in urban areas. African woolly-necked storks are well-liked in KwaZulu-Natal and both feeders and none-feeders appreciate their presence. Findings that feeders were most often motivated by personal pleasure and the opportunity to see the African woolly-necked storks (Chapter 3) at close range hints at the value of garden feeding of wild animals in providing an accessible experience of wildlife to a human population increasingly disconnected from nature (Cox and Gaston 2016). Having highlighted that some feeders fed inappropriate food such as bread and processed meat that could harm these birds especially nestlings (Chapter 3, Wilcoxon et al. 2015), I formulated a proposed feeding guideline for storks (Appendix 3.2). I hope

that these observations will inform future monitoring and guidance related to African woolly-necked stork garden feeding.

African woolly-necked storks are known to be sensitive to human disturbance especially during the nesting season. I was interested to know if these birds are breeding in suburban areas of KwaZulu-Natal or are only utilising anthropogenic food and nest in natural/rural habitats (Chapter 4). I found that African woolly storks have successfully established breeding sites suburban areas in KwaZulu-Natal, South Africa (Chapter 4). I identified 30 active nests through public outreach and vehicle surveys. By comparing used nest sites to randomly chosen non-used nest sites, we determined which features of the nest tree and surrounding habitat influenced their nest-site selection (Chapter 4). Most preferred nesting trees were exotic trees and located in front- or backyards of single-family houses in private residences (Chapter 4). The availability of tall and matured introduced trees into urbanised landscapes trees has contributed to the establishment of African woolly-necked stork breeding sites in suburban areas by providing suitable nest trees that were previously unsuitable for breeding (Chapter 4). The level of human disturbance did not appear to be a factor in nest selection. For example, three nests overhung two-lane suburban roads with almost constant human disturbance from both pedestrians and cars. The shift in nesting sites from natural places to anthropogenic structures in suburban environments may reflect the ability of birds to adapt to urban ecosystems (Wang et al. 2008). This study contradicts the existing perception about the species' sensibility to human disturbance during the nesting season.

After determining that the African woolly-necked storks successfully nest in suburban areas and mainly in domestic gardens and knowing that they widely utilise supplementary food, I sought to find the type of food provisioned to nestlings and general breeding behaviour of this species in an urbanised environment (Chapter 5). African woolly-necked storks provisioned their

nestlings with both natural and anthropogenic food in suburban areas of KwaZulu-Natal during breeding season. However, Amphibians, particularly guttural toads (*Amietophrynus gutturalis*), were the main prey of the African woolly-necked stork nestlings (Chapter 5). This suggests that although African woolly-necked storks utilise anthropogenic food, they still forage for natural food especially for nestlings (Chapter 5). The variation in diet and opportunistic use of locally abundant prey within suburban areas underscores the plasticity of African woolly-necked feeding behaviour. This plasticity may in part explain this stork's ability to occupy a wide variety of habitats in KwaZulu-Natal.

This study provides clear evidence that African woolly-necked storks in KwaZulu-Natal have adapted well to urbanisation to the point of thriving in this challenging environment. The recovery of the African woolly-necked storks in South Africa is a truly successful conservation story. Their expansion into human-dominated landscapes offers us a remarkable opportunity for studying a species in a post-recovery state as well as its potential to actually become overabundant in some areas. Many of the outcomes of this thesis will have implications to other species within suburban areas especially in South Africa.

6.2 Recommendations and future research

Along with foraging opportunities, availability of suitable nest sites generally appears to be the most limiting factors in bird populations (Marzluff 2001, Lowry et al. 2012), and the case of African woolly-necked storks in South Africa is no exception. The results from our analysis of nest-site characteristics enabled the formulation of several management recommendations. First, maintenance and protection of tall mature nesting trees like eucalyptus, pine and forest-Natal mahogany tree, especially in and around suburban areas, is essential for suburban-breeding storks.

The proposed protection of eucalyptus and pine trees might be controversial because these trees are invasive in South Africa. However, the removal or eventual death of existing nest trees could decrease suitable nest sites for African woolly-necked storks in the suburban landscape in South Africa. When possible, native trees that will grow sufficiently large and tall should be planted. Particular attention should be given to the numerous nest trees found in inhabited buildings and residential areas, since these nests are much more prone to disturbance because landowners have rights to cut down trees on their property. We therefore propose that all households should be requested to conserve active nest trees. Water bodies remain as fundamental to include in any conservation initiative of the African woolly-necked storks, and a distance of 1 km within breeding sites seems to be a reasonable target figure to manage such habitats. We propose maintenance of swimming pools and other artificial water sources in suburban areas. Wherever practical, potentially dangerous overhead power lines should be buried because power lines are used for perching, roosting and nesting by African woolly-necked storks in our study areas. It is highly advisable that processed meat is not fed to African woolly-necked storks especially during breeding as it may cause lethal effects to chicks: alternatively, raw meat such as chicken may be fed. Cooperation and involvement of landowners and stakeholders is crucial as human populations continue to expand, and close monitoring of African woolly-necked storks responses to such changes will be key to maintaining a fair equilibrium.

Overabundance of African woolly-necked storks in suburban areas may result in people losing tolerance to the point of this species becoming a nuisance to land-owners and leading to increased human-wildlife conflict. Therefore, population numbers of African woolly-necked storks should be monitored to avoid unsustainable population. Of concern were the cases of inappropriate food being fed to African woolly-necked storks and the number of incidences of

them having leg deformities. Further studies need to be conducted to determine the magnitude of these negative impacts. Future studies should look into aspects of reproduction success, post-fledging survival and movement of breeding pairs in order to have a more complete understanding of the dynamics of this population. Studies should also look at movement patterns and home ranges of the African woolly-neck storks within an urban environment. Environmental education programs could be essential to ensure the persistence of the populations.

6.3 References

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Appendix S6.1

FEEDING AFRICAN WOOLLY-NECKED STORKS

A proposed practice guide for landowners in South Africa

The African woolly-necked stork (AWN stork) is a large beautiful bird easily identifiable by its white woolly neck, with the rest of the plumage black. In South Africa this spectacular waterbird species was once endangered due to habitat loss and degradation. Thanks to intensive conservation efforts, AWN storks are once again a familiar sight especially in suburban areas of KwaZulu-Natal.



In the wild, AWN storks feed on aquatic invertebrates, amphibians, reptiles and small mammals. AWN storks successfully forage for natural food in domestic gardens, open green spaces and golf courses. Many people like to feed AWN storks mainly for the opportunity to see them close. If AWN storks do not have a balanced diet they can suffer from serious dietary deficiencies, which may even lead to death in some cases.

If you DO decide to feed African woolly-necked storks, following these guidelines will help to ensure that any problems associated with supplementary feeding are minimised:

- i. Preferably, feed only raw meat such as chicken.
- ii. Only put out small amounts of food. This will help to ensure that AWN storks will not become dependent on the food you are supplying, and will continue to feed naturally.
- ii. Do not feed processed meats (which have potentially harmful additives especially for nestlings).
- v. Do not increase the amount of food you put out when more storks visit – this will prevent artificially high numbers of AWN stork visiting your area.
- v. Regularly wash and disinfect all containers and equipment used for feeding AWN stork.

