Population ecology of Woolly-necked Storks (*Ciconia microscelis*) in a South African mosaic landscape

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Submitted in fulfilment of the academic requirements for the degree of

Doctor of Philosophy

in the Discipline of Ecological Sciences

School of Life Sciences

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

Pietermaritzburg Campus

2024

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ABSTRACT

As large, aquatic birds, storks (family Ciconiidae) and their population dynamics can provide useful information about how wildlife respond to changing land use. There are 20 extant stork species with varying conservation statuses, yet few species have received much research and conservation attention. Although storks can act as indicators for their usual wetland habitats, there is increasing evidence that some species are ecologically flexible and can persist in human-altered landscapes. This study aimed to use the African Woolly-necked Stork (*Ciconia microscelis*; hereafter, 'woollyneck') in South Africa as a case study of urban wildlife colonisation and behavioural plasticity. Previously a rare and secretive species in South Africa, the woollyneck has expanded its range southward in KwaZulu-Natal over the past few decades, especially colonising urban and mixed use landscapes. We investigated how two important components of population dynamics–reproduction and nata dispersal–could have facilitated rapid population expansion in KwaZulu-Natal, and how spatially resident woollynecks use the urban environment.

Firstly, we studied the urban breeding ecology of woollynecks by monitoring 112 nesting attempts during two nesting seasons in KwaZulu-Natal. We described previously unknown aspects of the natural history of woollynecks, including clutch size, breeding phenology, breeding metrics, and nest site fidelity. Fecundity in the two study seasons was very different (1.4 nd 0.7 fledglings per pair), suggesting that in some years, woollynecks produce a high number of chicks that may compensate for years of poorer reproductive output. The probability of fledging at least one nestling was significantly related to rainfall and egg-laying date, with higher success probability earlier in a breeding season and when rainfall was higher.

Secondly, we investigated the dispersal of immature woollynecks using high-resolution telemetry and low-resolution colour-ring mark-resight. Immature woollynecks had large areas of spatial use, and these areas mostly decreased as they got older. From telemetry, we found the farthest distance moved from a natal nest site was 220 km. Colour-ringed woollynecks were resighted an average of 26.5 km from their natal site, with some as far as 98 km.

Finally, we used telemetry to understand how resident adult woollynecks moved in an urban landscape. Adults had very small home ranges ($\bar{x} = 4.37$ km^2) and travelled very short distances on average (0.82 km) from the nest while breeding. Apparently, the abundance of nesting trees and food in the form of amphibians in residential gardens and supplemental anthropogenic food has allowed adult woollynecks to become highly sedentary following the colonisation of urban mosaic landscapes in KwaZulu-Natal.

The results of this study provide novel insight into (1) how KwaZulu-Natal’s woollyneck population could have expanded so rapidly (i.e., high breeding success and natal dispersal), and (2) how the established urban population of woollynecks move in an urban mosaic landscape. Given the abundance of resources for woollynecks in such landscapes, it is possible the recruitment of a high number of young storks into the population and their far dispersal movements will facilitate the continued expansion of the population southward into Eastern Cape Province and inland in KwaZulu-Natal. In contrast to their historical description as shy and secretive, woollynecks in KwaZulu-Natal have demonstrated unexpected behavioural plasticity in their adjustment to an urban mosaic environment, which suggests other species may have similar capacity that has yet to be observed.

PREFACE

The data described in this thesis were collected in KwaZulu-Natal, Republic of South Africa, from August 2022 to November 2024. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof Colleen T. Downs and Prof Sandi Willows-Munro.

This thesis, submitted for the degree of Doctor of Philosophy in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, 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.

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Jonah Gula

November 2024

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

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Prof Colleen T. Downs

Supervisor

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DECLARATION 1 - PLAGIARISM

I, Jonah Gula, 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.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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    a. Their words have been re-written but the general information attributed to them has been referenced
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DECLARATION 2 - PUBLICATIONS

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

PUBLICATION 1 (Formatted for *Biological Conservation* –published)

The state of stork research globally: A systematic review

J Gula, KSG Sundar, S Willows-Munro, & CT Downs

Author contributions:

JG conceived the paper with KSGS, SW-M, and CTD. CTD sought funding. JG collected and analysed data, and wrote the paper. KSGS, SW-M, and CTD contributed valuable comments to the manuscript.

PUBLICATION 2- (Formatted for *Ibis* – not yet submitted)

Breeding ecology of Africa's only known population of urban Woolly-necked Storks (*Ciconia microscelis*)

J Gula & CT Downs

Author contributions:

JG conceived the paper with CTD. CTD sought funding. JG collected and analysed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

PUBLICATION 3- (Formatted for *Ostrich* – not yet submitted)

Natal dispersal of immature African Woolly-necked Storks (*Ciconia microscelis*) in an urban-colonised area of South Africa

J Gula & CT Downs

Author contributions:

JG conceived the paper with CTD. CTD sought funding. JG collected and analysed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

PUBLICATION 4- (Formatted for *Urban Ecosystems* – not submitted)

Spatial use of adult African Woolly-necked Storks (*Ciconia microscelis*) following urban colonisation in South Africa

J Gula & CT Downs

Author contributions:

JG conceived the paper with CTD. CTD sought funding. JG collected and analysed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

Signed: [redacted]………………………

Jonah Gula

November 2024

ACKNOWLEDGEMENTS

I am eternally grateful to Prof Colleen T. Downs for her over-and-above support throughout this project and my other research. I don't know where I would be without her. I also thank Prof Sandi Willows-Munro for her support with lab-related work. I remain amazed at the kindness of strangers that I have experienced during this PhD. Hundreds of members of the public graciously assisted in my project by reporting nests and colour-ringed storks, allowing me to trap storks and/or monitor nests at their homes, and assisting with nest monitoring when I was absent. Without them, this project absolutely would not have been possible. In particular, I want to thank two of those strangers who have since become precious friends: Liz van Rooyen and Welma Brouwer.

I am grateful for Maryanne Anderson's and Ntando Makhathini's assistance with capturing storks. I am especially indebted to Themba Manzini for his incredible tree-climbing skills, which allowed me to access nestling storks, even in nests that would seem impossible to reach. Thanks to Duncan and Wendy Gillon for their assistance in that endeavour, too. A big thank you to my long-time mentor and friend, K.S. Gopi Sundar, for challenging me to think critically and for his contributions to brainstorming some approaches to this research and beyond. Thanks to my other friends who have been supportive since I came to UKZN and who have always been fun in the field: Dr Lehlohonolo Adams, Dr Mahlatse Mashaphu, Dr Nasiphi Bitani, Dr Matthew Burnett, Lwandile Ngozi (a.k.a. Belmokhtar), Sboniso Magoso, and Kholosa Magudu. Finally, thanks to my wife, Ziphezinhle, for being supportive and understanding during the final phase of this project. Finally, I dedicate this dissertation to my late aunt, Loretta Gosting, who was not able to see me finish this work but who was always one of my greatest supporters in my journey to this PhD.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION

1.1 Background

In 2007, for the first time in history, more humans lived in urban areas than rural areas globally, and by 2030, it is predicted that 60% of people will be urban (United Nations 2019). As a consequence, urban land expansion is happening at an unprecedented rate, with some projections suggesting an addition of 1.1–3.6 million km^2 of urban land by 2100 (Gao and O'Neill 2020). Such significant changes in land use have and will continue to have effects on biodiversity (Gallo et al. 2017, Mcdonald et al. 2008, Ortega-Álvarez and MacGregor-Fors 2009). However, the growing body of research on these effects has demonstrated how variable they can be, as influenced by factors such as species-specific history (Møller et al. 2012), socio-economics of urban areas (Kuras et al. 2020), urban greenspace management (Threlfall et al. 2017), habitat characteristics (Iknayan et al. 2022), and species-specific ecological characteristics (Møller 2009, Rawal et al. 2021), to name a few.

Wildlife in urbanised areas face novel challenges and/or opportunities related to habitat, food, and breeding compared with their natural-habitat counterparts. Whereas some species benefit from habitat creation in urban environments (Hara et al. 2018, Mayer and Sunde 2020, Møller et al. 2012), the loss or degradation of habitat for others leads to population declines and/or local extirpations (Dri et al. 2021, Mitrovich et al. 2018, Stoner et al. 2023). However, the relationship between habitat modification and persistence in urban areas can be nuanced and species-specific, too (Nagy and Rockwell 2013, Robinson et al. 2018, Stark et al. 2020). Urbanisation can also result in declines in food availability and/or quality for some species (Francis et al. 2021, Murray et al. 2015, Narango et al. 2018) while access to novel food sources and conditions (natural and/or anthropogenic) can positively effect others (Evans and Gawlik 2020, Oro et al. 2013, Rodríguez et al. 2021, Suri et al. 2017). As with habitat modification, food-related effects can also be nuanced. For example, anthropogenic food quality affects adults and juveniles in different ways (Catto et al. 2021). Some species experience enhanced breeding success in urban environments (Kettel et al. 2019, Minias 2016, Stracey and Robinson 2012) while others fall into ecological traps from negatively affected breeding outcomes (Demeyrier et al. 2016, Kettel et al. 2018, Meyrier et al. 2017). Thus, it is clear that there are variable tradeoffs for an urban lifestyle, and a one-size-fits-all conclusion about the impacts of urbanisation on wildlife is not in line with the evidence from the field of urban ecology.

Some of the most rapid urban land expansion is occurring in Africa (Gao and O'Neill 2020), where 59% of the human population is predicted to live in urban areas by 2050 (United Nations 2019). Despite this, there is growing evidence of wildlife persisting in, adapting to, and even colonising African urban areas (Downs et al. 2021, Henriques et al. 2018, Holbech and Cobbinah 2021, Pomeroy and Kibuule 2017, Yirga et al. 2017), although this urban ecology work has been biased to South Africa (Awoyemi and Ibáñez-Álamo 2023). Birds in particular have been well-studied in urbanising environments in Africa, especially raptors and passerines, likely because they have most readily colonised or persisted in modified landscapes (Catto et al. 2021, Matthew et al. 2024, McPherson et al. 2016, Suri et al. 2017). However, research around the world has increasingly shown that different waterbird taxa may exploit resource patches within an urban habitat matrix, too (Evans and Gawlik 2020, Hara et al. 2018, McKinney and Raposa 2013, Pais De Faria et al. 2023, Rawal et al. 2021). In Africa, few studies on waterbirds, especially large species, have focused on urban ecology, with two exceptions being the Hadeda Ibis (*Bostrychia hagedash*), in South Africa (Duckworth and Altwegg 2014, Singh and Downs 2016) and the Marabou Stork (*Leptoptilos crumenifer*) in Uganda (Pomeroy and Kibuule 2017, Pomeroy and

Kibuule 2021). As a result, there remains an important knowledge gap about how African waterbirds respond to urbanisation.

1.2 Study area

This study was conducted in urban and suburban areas of the southern half of KwaZulu-Natal Province, South Africa (Figure 1.1). Specifically, the study was in the municipalities of eThekwini, Mkhambathini, Msunduzi, Richmond, uMngeni, uMshwathi and uMdoni, but primarily between the cities of Durban (8 m a.s.l.) and Howick (1060 m a.s.l.). This region is characterised by a subtropical climate, but a gradient exists across the study area from the coast to higher elevations inland. Mean annual rainfall in the city of Durban (eThewkini Municipality) is 893 mm, and mean annual minimum and maximum temperatures are 13.7° C (July) and 27° C (February), respectively (https://en.climate-data.org/africa/south-africa/kwazulu-natal/durban-511/). Mean annual rainfall in Howick (uMngeni Municipality) is 1074 mm, and mean annual minimum and maximum temperatures are 4.5° C (July) and 25° C (Feburary), respectively (https://en.climate-data.org/africa/south-africa/kwazulu-natal/howick-27052/). The eThewkini, Msunduzi, and Umdoni municipalities are mosaics of mixed land use, with varying levels of urbanisation (commercial and residential use) interspersed by green spaces (gardens, parks, conservancies, and nature reserves). The Mkhambathini, Richmond, uMngeni, and uMshwathi municipalities are characterised by greater rural area and more limited urbanisation than the other municipalities. In the 2022 South African census, population density across the study area varied from 50 people/km^2 in the Richmond Municipality to 1,851 people/km^2 in the eThekwini Municipality (Statistics South Africa 2023).

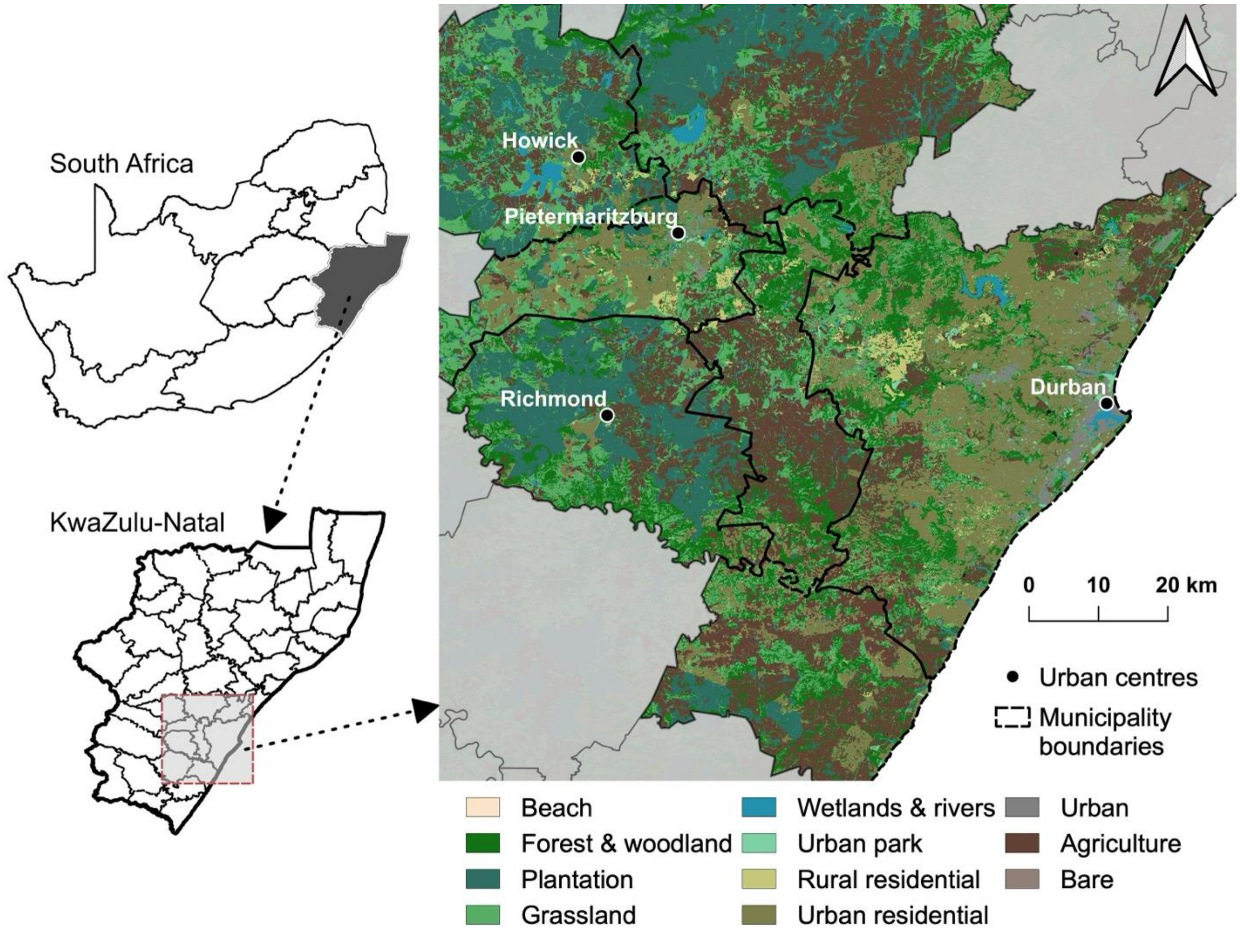

Figure 1.1: The study area in south-central KwaZulu-Natal, South Africa, which included seven municipalities.

1.3 Problem statement

Until recently, the scant literature on the African Woolly-necked Stork (*Ciconia microscelis*; hereafter, woollyneck) generally described it as shy and easily disturbed, particularly during breeding, and usually uncommon or rare in natural wetlands (Brown et al. 1982, Hancock et al. 1992, Scott 1975). In the 1980s, the total breeding population of woollynecks in South Africa was thought be around 30 pairs (Brooke 1984). However, in the last three decades, the woollyneck has rapidly expanded–geographically and demographically–in KwaZulu-Natal Province, South

Africa, especially in human-modified landscapes such as urban and agricultural areas (Allan 2012, Thabethe 2018). Now woollynecks are common residents of many urban areas in KwaZulu-Natal (Figure 1.2), where groups of dozens of storks may be supplementally fed at residential homes or take advantage of human refuse sites (Thabethe and Downs 2018; JG, pers. observ.), thus representing urban exploitation that is unparalleled elsewhere in the species' range. However, it remains unknown how a novel urban lifestyle affects aspects of woollyneck population ecology, such as breeding success and spatial ecology. This study is not only the first to explore the urban ecology of Africa's only known urban woollyneck population, but also the first to study the species' ecology anywhere in Africa. As a result, this study importantly contributes to species-specific knowledge as well as to the growing understanding of how urbanisation affects wildlife populations in subtropical regions.

Figure 1.2: Woolly-necked Storks are now common garden birds in many areas of urban KwaZulu-Natal, South Africa, today.

1.4 Aims and objectives

The aim of this study was to understand the population ecology of Africa's first known urban woollyneck population and how the historic population expanded rapidly into urban landscapes. The objectives were to:

1. Determine the breeding productivity of an urban breeding population of woollynecks and factors that affect productivity.
2. Describe the dispersal movements of the immature cohort of urban woollynecks.
3. Describe the spatial use of resident adult woollynecks in urban areas.

1.5 Structure of the thesis

The main body of this thesis is organised as manuscripts prepared for publication in peer-reviewed journal articles. The first chapter (Chapter 1) is the Introduction, which provides the literature review of the concepts covered in this study. The second chapter (Chapter 2) is a systematic literature review of stork species globally. The next chapters (Chapters 3, 4, and 5) each cover a specific aspect of urban woollyneck ecology. Because of each chapter is intended for separate publication, there is a certain degree of repetition, especially in the methods section. However, this is deemed to be of little concern as this format allows the reader to read each chapter separately without losing the overall context of the thesis. Chapter 2 investigated the scientific knowledge on all 20 species of storks in the family Ciconiidae. The objective of this chapter was to synthesize published information on storks, including geographic biases and topical coverage in research. Chapter 3 investigated the breeding ecology of woollynecks in urban areas of KwaZulu-Natal, South Africa. The objective of this chapter was to determine basic breeding parameters and what factors influence breeding success. Chapter 4 investigated the dispersal of immature woollynecks in urban areas of KwaZulu-Natal. The objective of this chapter was to understand the movement of immature woollynecks upon independence and how this contributed to population expansion. Chapter 5 investigated the spatial ecology of adult woollynecks in urban areas of KwaZulu-Natal, with the objective of understanding the extent of movement in a human-altered landscape. Finally, Chapter 6 provides a synthesis of the study's main findings and their implications as well as recommendations for future research.

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CHAPTER 2

The state of stork research globally: a systematic review

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Published in *Biological Conservation* in April 2023:

https://doi.org/10.1016/j.biocon.2023.109969

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Running header: State of global stork research

2.1 Abstract

Storks are a conspicuous pan-global freshwater flagship taxon with 20 extant species, all of which have been accorded IUCN Red List status. Red List assessments use a combination of scientific evidence and expert inputs to develop species-level status, but there is little careful evaluation of whether these assessments are comparable across species. Using standard literature databases, we compiled and analysed patterns of research in peer-reviewed literature for all 20 stork species. Our search yielded 989 publications between 1950 and 2022, showing bias in both the coverage of species (66% covered three stork species) and geographical locations (53.8% from Europe and the United States of America) despite the highest stork species richness being present in Africa and Asia. Publications on storks, especially from Asia, have increased over time, with 81% of all studies published since 2000. Most stork research focused on breeding ecology, but was skewed towards only three species. Growing research in Asia showed significant populations of several stork species amid farmlands, suggesting the need to advance similar research in anthropogenically modified landscapes elsewhere. The population and behaviour ecologies of 15 (75%) stork species remain unstudied. Our review showed scientific evidence varying enormously across stork species, with sparse scientific understanding being the norm. Red List statuses must be made more robust for storks, especially highlighting data-deficient species to help prioritize conservation research, particularly in Africa and Asia, thereby facilitating the development of accurate status assessments for these species.

Keywords: bias; Ciconiidae; conservation; farmland; waterbirds; wetlands

2.2 Introduction

Waterbird populations are generally thought to be in decline globally, especially in Africa, Asia, and South America (Delany et al. 2010). Given that waterbirds can be used reliably as indicators of environmental change (Amat and Green 2010, Kushlan 1993), their global trends may underscore the state of wetland habitats and the landscapes that they inhabit. It is increasingly recognised that a one-size-fits-all approach is insufficient for addressing conservation issues related to waterbird conservation, and that region- and location-specific knowledge about waterbirds is required for successful habitat and population recovery (Kittur and Sundar 2021, Ma et al. 2010, Tománková et al. 2013). However, this requires ecological data about specific species and communities, which may be unavailable for some taxa and in some parts of the world where research has been limited.

The storks (family Ciconiidae) comprise 20 species globally, most of which have subtropical or tropical distributions (Figure 2.1). A coarse assessment of global conservation priorities for storks decades ago identified significant knowledge gaps about most species, especially in Asia (Luthin 1987). Over thirty years on, there is no assessment of the state of the science for the taxon, although significant strides have been made in understanding conservation requirements of several species (e.g., Ghimire et al. 2021, Kittur and Sundar 2020, Sundar 2011, Sundar et al. 2019, Win et al. 2020). Most stork species globally are not considered threatened on the IUCN Red List, which uses a combination of science and expert advice to determine species status. Despite the relatively wide use of Red List status to inform global and national policies, there have been few careful assessments of whether statuses accorded to species, or taxa like storks, are reliable and based on evidence that is comparable across species. The Red List declares a small list of species as Data Deficient, but many additional species are accorded a confident conservation status despite a relatively low understanding of the species' requirements, threats, and an absence of population metrics. In some cases, species status has been changed based on broad suggestions or assumptions regarding potential threats to the species without sufficient documentation, as is required according to the Red List procedures (Mrosovsky 1997).

The Red List for birds, which BirdLife International administers, uses an online forum where interested people can contribute information towards understanding species threats and population status (Hoffmann et al. 2008). These comments are then compiled by Red List coordinators to develop basic ecological information such as population sizes, threats, and other related aspects. Robust statistical analyses are then applied to this information, especially focusing on metrics such as trends in populations, breeding success, and habitat associations that are collectively evaluated before assigning a status. Species with a Red List status are therefore assumed to have basic ecological information that has been used to ascertain their status and inform about threats. However, there have been few independent assessments of whether species statuses are indeed based on at least a minimal understanding of species habits and requirements, and whether there is useful data to base changes in the status of some species over time. As large, conspicuous, and charismatic waterbirds, storks are an ideal representative group for wetland conservation, and several species have already been used to demonstrate their value as ecological indicators of environmental contamination or habitat restoration and as representatives of ancient agricultural practices (Frederick et al. 2009, Goutner and Furness 1998, Kittur and Sundar 2021, Naito et al. 2014, Tobolka et al. 2012). Therefore, advancing our scientific knowledge of storks can be an important way to advance the conservation of their habitats and the species with which they share them. This group is also useful to test the efficacy of the Red List status assignments since all the species of this group have been accorded a status.

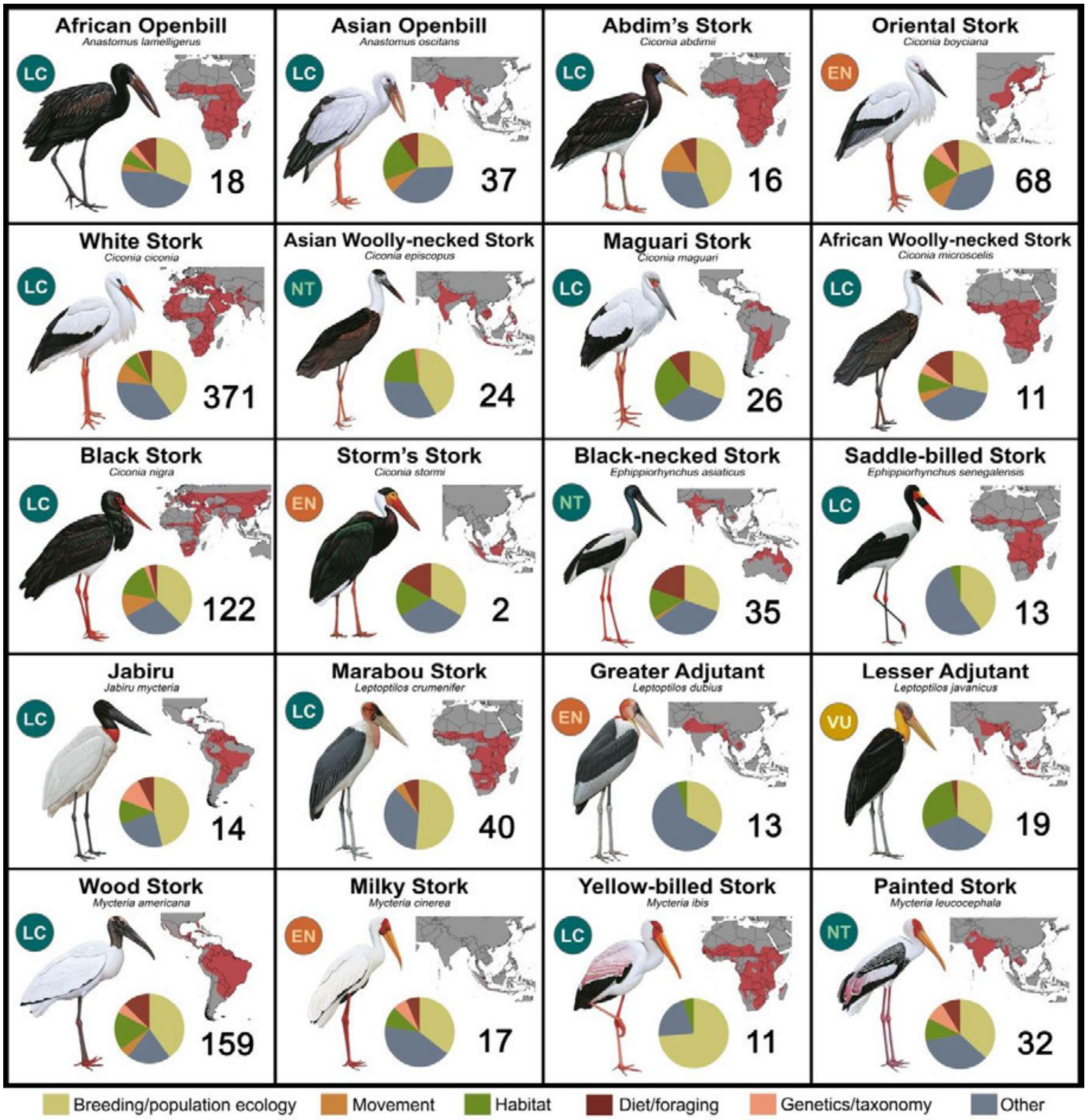

Figure 2.1: The 20 species of storks in the family Ciconiidae, each with their IUCN Red List status (LC=Least Concern, NT=Near Threatened, VU=Vulnerable, EN=Endangered), geographic range (source: IUCN/BirdLife International), number of publications identified in the literature search from 1950 to 2022, and a pie chart showing the proportion of publications on six broad study topics (colour legend at bottom). Illustrations used with permission from Birds of the World (Cornell Lab of Ornithology).

We conducted a systematic literature review of the storks of the world to understand the state of stork research globally and to understand where research should be prioritised to improve status assignments and conservation outcomes for specific species and their habitats. We expected publications on storks globally to have increased over time, primarily driven by a bias towards stork species found in Europe and North America. Consequently, we expected tropical species to be the least studied and to have the most uncertain population statuses. Finally, based on the results, we aimed to highlight important species-specific gaps in scientific knowledge that will help prioritise research and improve Red List status assignments on storks moving forward.

2.3 Materials and methods

In the Google Scholar (https://scholar.google.co.za/) and Scopus databases, we used the programme Publish or Perish (Harzing 2022) to search peer-reviewed literature for information on storks from January 1950 to June 2022. We searched titles and text using the scientific names of the 20 stork species globally, including historic nomenclature. Additionally, we searched titles for common names, including variations on English spellings (e.g., “woollyneck” vs. “woolly-necked” or “saddlebill” vs. “saddle-billed”). Some results, particularly for the White Stork (*Ciconia ciconia*) in eastern Europe and Asian Openbill (*Anastomus oscitans*) in south and southeast Asia, were in journals that clearly were not robustly peer-reviewed, and these were excluded from our analyses. We chose not to limit our searches to journals with impact factors so as not to exclude important bodies of work outside these sources. We excluded literature that merely reported on occurrence, such as notes reporting the first confirmed breeding in a province, general presence/absence surveys of birds, etc., and studies on storks in captivity unless the topic related to anatomy or physiology that was also relevant in the wild (e.g., disease). We also did not consider publications that reported species inventories or multi-species analyses that did not explicitly report species-specific information. Non-English results were only considered in the title searches, given the preponderance of irrelevant results in text searches and the difficulty in translating these. We only considered non-English publications if the full-text document could be translated using Google Translate.

After filtering the results, we identified the country or countries where each stork study occurred to assess the geographic distribution of research for all 20 stork species. We used the publication year of each study to assess temporal trends in research, too. To better understand knowledge gaps, we categorised each publication into 19 topics (Figure 2.2) based on the subjects of the study. Studies were categorised into a maximum of four topics because some publications covered multiple aspects of biology, ecology, or conservation. Finally, we compiled estimates of breeding success (e.g., hatching/fledging success or fecundity) reported in publications. We report the range of estimates in studies over multiple years or areas if these were available; otherwise, we report the mean as presented in the respective publication. We calculated estimates when success rates or fecundity were not explicitly reported, but raw data were presented. Some studies were excluded from this summary because full-text publications could not be located from which to extract estimates not explicitly stated in abstracts. We used descriptive statistics to show trends in research. Finally, we summarised the trends in IUCN status assessments for the 20 stork species on the Red List website (IUCN 2021).

2.4 Results

Our literature search on the 20 stork species of the world produced 989 peer-reviewed publications from January 1950 to June 2022 (species-specific reference lists can be found at https://docs.google.com/spreadsheets/d/1bdUrpJ9dydjU90-eIycC6isQmOwzIOJtGnUw878t4fU/edit?usp=sharing), some of which covered multiple species. Publications were heavily biased toward three species, the White Stork, Wood Stork (*Mycteria americana*), and Black Stork (*C. nigra*), which together accounted for ~66% of all publications (Figure 2.1). Publications on the White Stork (37.5%) alone made up more than one-third of all the results. Consequently, publications were heavily biased toward Europe and several countries in the Americas (Figure 2.3). Field studies in Europe and the United States of America (USA) accounted for 53.8% of all publications. Only two publications were on the Storm's Stork (*C. stormi*), and other poorly studied storks included the African Woolly-necked Stork (*C. microscelis*) and the Yellow-billed Stork (*M. ibis*), which had 11 publications each. Despite having the greatest diversity of stork species, Africa (8 species) and southeast Asia (8 species) had much fewer publications than regions with much fewer species (Figures 2.1 and 2.3).

Globally, publications on storks have increased dramatically over time, and 2021 saw the highest number of publications on storks in history (Figure 2.4). Of the 989 publications we identified, 81% have been published since 2000, while 51% were published since 2010, showing increased publications, especially in the last decade. When comparing continents, Europe had 89% of publications published since 2000, and 51% since 2010, while North America had 58% since 2000 and 28% since 2010. For South America, 72% were published since 2000 and 52% since 2010. Sub-Saharan Africa had 63% of publications published since 2000 and 43% since 2010. In contrast, Asia had 88% of publications published since 2000 and 62% since 2010. Asia was the only continent where publications have been continually growing each year.

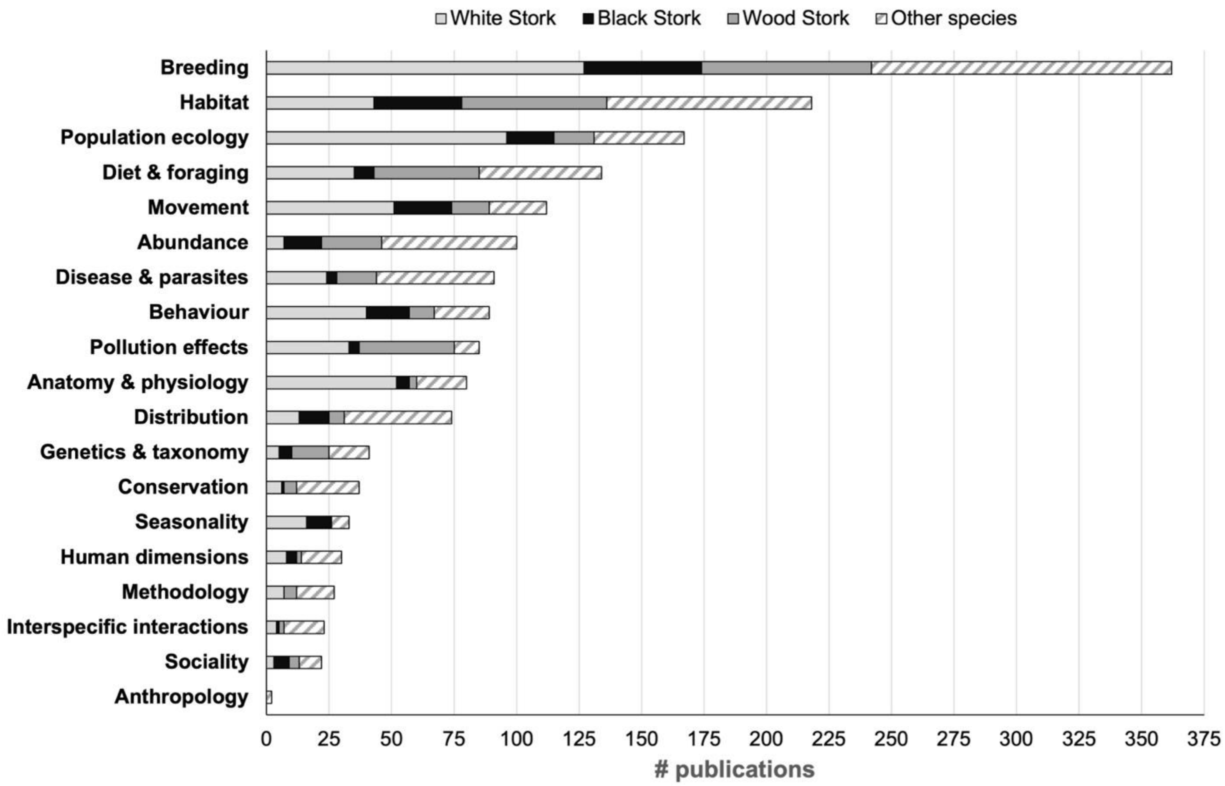

Figure 2.2: Number of publications from January 1950 to June 2022 that covered different topics on storks showing how three stork species dominated many topics.

Globally, publications on storks have increased dramatically over time, and 2021 saw the highest number of publications on storks in history (Figure 2.4). Of the 989 publications we identified, 81% have been published since 2000, while 51% were published since 2010, showing increased publications, especially in the last decade. When comparing continents, Europe had 89% of publications published since 2000, and 51% since 2010, while North America had 58% since 2000 and 28% since 2010. For South America, 72% were published since 2000 and 52% since 2010. Sub-Saharan Africa had 63% of publications published since 2000 and 43% since 2010. In contrast, Asia had 88% of publications published since 2000 and 62% since 2010. Asia was the only continent where publications have been continually growing each year.

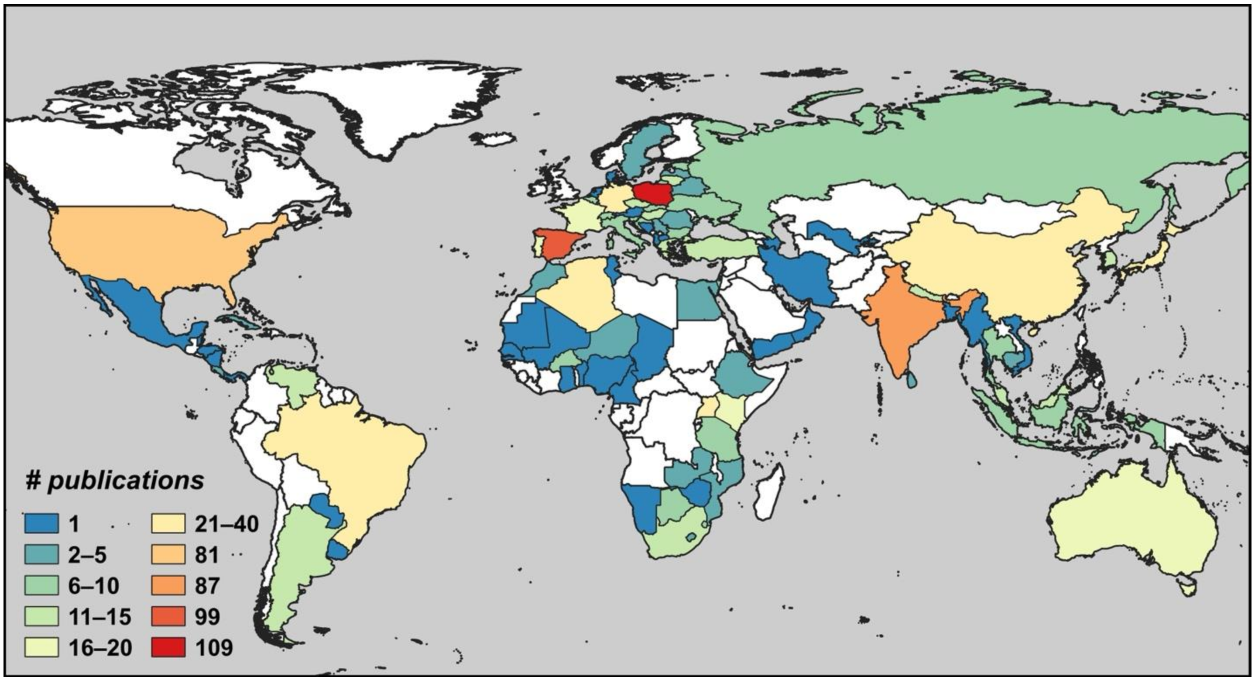

Figure 2.3: Global distribution of peer-reviewed publications on the 20 stork species of the world from January 1950 to June 2022. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

Few stork species and populations have been the subjects of a long-term study. Research in Poland and Spain has produced the highest number of publications with long-term data (Figure 2.3) because their populations of White Storks and Black Storks have been extensively studied over the last 20 years. The White Stork in Germany has similarly been well-studied during the same time. Consequently, there is significant knowledge about population dynamics in several parts of Europe. For the Wood Stork, 37% of publications on the species were based in the Florida Everglades, USA, because of long-term research centred on the ecological restoration of these wetlands. The threatened status of the Oriental Stork (*C. boyciana*) has led to consistent research on the species in China, South Korea, and Japan over the last 20 years. Reintroduction efforts in Japan have particularly driven research on some aspects of population and habitat ecology. The Black-necked Stork (*Ephippiorhynchus asiaticus*) and Painted Stork (*M. leucocephala*) in India are the only other Asian species that have been the subject of consistent research over many years, although primarily on the subjects of breeding and foraging. Finally, the Marabou Stork (*Leptoptilos crumenifer*) has been sporadically studied in urban areas of Uganda since the 1970s, but the research on population dynamics is now decades old.

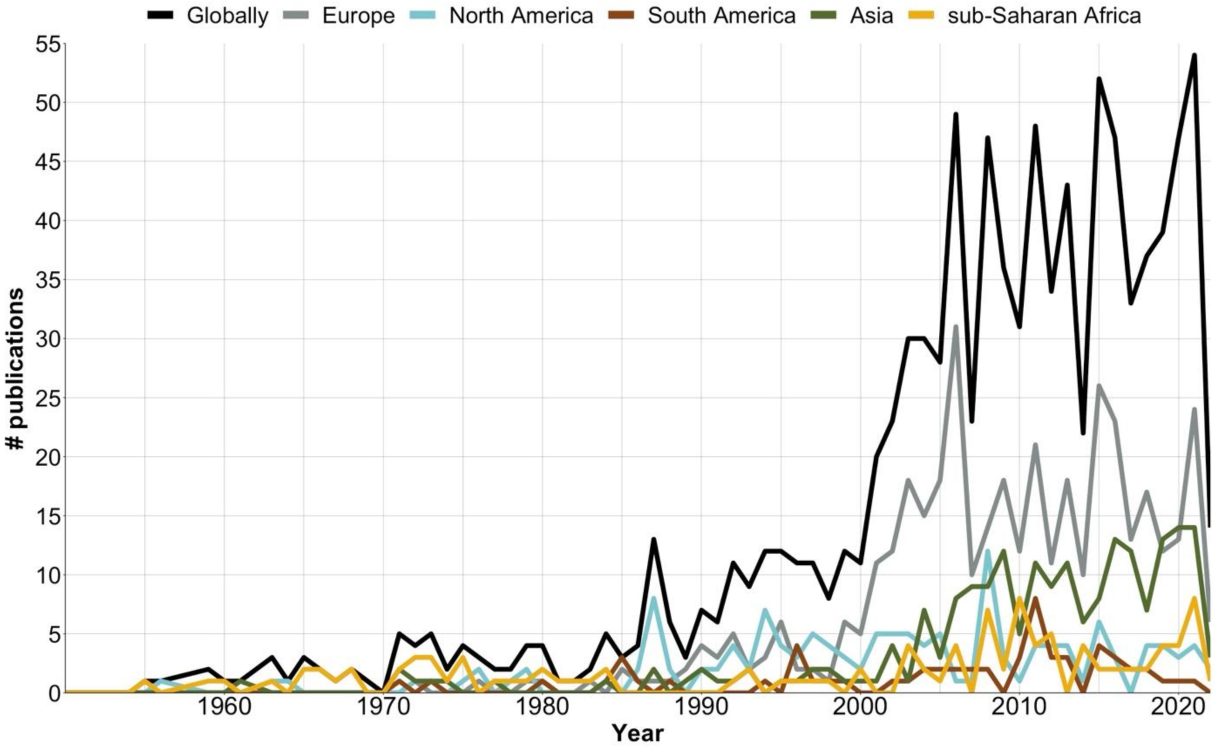

Figure 2.4: Annual trends in peer-reviewed publications on the 20 stork species globally and by continent between January 1950 and June 2022.

Table 2.1: Summary of breeding strategies and other findings in publications on the 20 species of storks globally from 1950 to 2022.

Species	**# countries with publications (% of range countries)**	**Studied in agricultural or urban areas?**
African Openbill *Anastomus lamelligerus*	10 (28%)	X
Asian Openbill *A. oscitans*	7 (58%)	agricultural
Abdim's Stork *Ciconia abdimii*	9 (23%)	X
Oriental Stork *C. boyciana*	4 (67%)	agricultural
White Stork *C. ciconia*	55 (51%)	agricultural & urban
Asian Woolly-necked Stork *C. episcopus*	5 (33%)	agricultural
Maguari Stork *C. maguari*	5 (42%)	agricultural
African Woolly-necked Stork *C. microscelis*	4 (10%)	urban
Black Stork *C. nigra*	39 (38%)	agricultural
Storm's Stork *C. stormi*	1 (20%)	X
Black-necked Stork *Ephippiorhynchus asiaticus*	2 (15%)	agricultural
Saddle-billed Stork *E. senegalensis*	7 (19%)	X
Jabiru *Jabiru mycteria*	7 (44%)	X
Marabou Stork *Leptoptilos crumenifer*	9 (23%)	urban
Greater Adjutant *L. dubius*	2 (33%)	X
Lesser Adjutant *L. javanicus*	7 (54%)	agricultural
Wood Stork *Mycteria americana*	10 (45%)	urban

Table 2.1 (continued).

Species	**# countries with publications (% of range countries)**	**Studied in agricultural or urban areas?**
Milky Stork *M. cinerea*	4 (100%)	X
Yellow-billed Stork *M. ibis*	7 (16%)	X
Painted Stork *M. leucocephala*	4 (36%)	agricultural & urban

Some aspect of breeding was covered in 37% of stork publications, making it the most prominently featured topic (Figures 2.1 and 2.2). However, 67% of these publications were related to the breeding of three species: the White Stork, Black Stork, or Wood Stork. Similarly, publications on these three species dominated the topics of habitat (62%) and population ecology (78%), which were the next most featured topics in publications after breeding.

The majority of stork species (n = 15, 75%) have publications from less than 50% of their range countries, and even the White Stork has only been studied in 54% of its range countries (Table 2.1). Breeding success has been estimated at least once for fifteen species in 95 publications. However, only 53% of these investigated how this important population parameter related to intrinsic or extrinsic variables (Supplemental information Table S2.1). Over half of the publications reporting breeding success were on the White Stork, and 74% were on the White Stork, Black Stork, and Wood Stork combined. Twelve stork species have been studied in anthropogenically modified mosaic landscapes, including agricultural or urban environments, although some to greater extents than others. Most of these studies have not found detrimental effects on storks in these environments, and in many cases, species experienced benefits.

Eleven stork species had their status changed to Least Concern in 2004 following the previous listing as Unknown. Among these species is the Jabiru, which was listed as Near

Threatened in 1988 and then Unknown between 1994 and 2004 before being reassigned as Least Concern. The African Woolly-necked Stork, which was listed as Least Concern in 2014, did not have previous status assessments and remains without any scientific population studies. The Black-necked Stork and Painted Stork were listed as Unknown until 2004, when they were seemingly arbitrarily uplisted to Near Threatened. Another species that saw unusual changes within a relatively short period was the Asian Woolly-necked Stork (*C. episcopus*). Its status was changed from Least Concern to Vulnerable in 2019 despite multi-year evidence provided on the online discussion forum showing stable populations in several locations. Following the publication of new evidence in a special section on the species in “*SIS Conservation*” (the publication of the IUCN Stork, Ibis, and Spoonbill Specialist Group), its status was downgraded from Vulnerable to Near Threatened in 2020. Recent studies have developed a population estimate for Asian Woolly-necked Stork based on multi-location, multi-year field studies. The new evidence-based estimate was nearly seven times the existing “guesstimate”. Studies also show breeding success of the species to be consistent and very high even in areas with high human densities and with long-term agriculture, contrary to the existing assumption until then that the species was threatened by agriculture. It is not, therefore, entirely clear why the downlisting was made to Near Threatened rather than to Least Concern, which was the status that the species previously had in the absence of field-based knowledge of its breeding status and habitat associations. The Milky Stork (*M. cinerea*) was uplisted from Vulnerable to Endangered in 2013 despite no scientific study on population size or trend to date, and seems to be based entirely on opinion. The remaining stork species have been accorded a confident status despite the fact that some, such as the Greater (*L. dubius*) and Lesser Adjutants (*L. javanicus*), used to be largely unstudied, but have literature documenting healthy, growing populations on south Asian agricultural landscapes. Population estimates for Asian and African stork species with no alternative source of reliable information have been derived from the Asian and African Waterfowl Censuses, volunteer activities where participants report bird counts at individual wetland sites. These population sizes do not appear to be based on any consistent repeatable method, and include the strong assumption that all these stork species are reliant on wetlands as their primary habitats.

2.5 Discussion

Our literature review is the first such effort for the stork family Ciconiidae and has highlighted significant taxonomic and geographic bias in published research. Until now, the knowledge of many stork species has been largely founded in non-peer-reviewed works, summary accounts, anecdotes that generally inform more about basic life history than habitat or population ecology (e.g., Hancock et al. 1992), or expert advice as part of the IUCN Red List process followed for birds. We found that most research on storks has been published in the last decade, and that there has been an encouraging increasing trend in Asia recently. Still, most species have been studied in only a small proportion of countries where they occur, suggesting that published research does not represent all populations. Given that the majority of stork species occur in tropical regions, the research bias toward the White Stork, Wood Stork, and Black Stork in developed, temperate countries has meant that research findings are not appropriately transferable to other species, creating important knowledge gaps for tropical species. It is tempting to use the large body of work produced on species found in the developed countries to inform study approaches elsewhere, but findings of requirements of stork species elsewhere, such as in Asia, underscore the importance of context-specific approaches.

The focus of this review on peer-reviewed publications left out knowledge contributed by dissertation research that was not published in peer-reviewed journals (e.g., Motalaote 1996), most notably Berdie's (2008) thesis on Storm's Stork habitat requirements, which is important for this poorly studied species. The program Publish or Perish did not produce results that included every known publication on storks, as evidenced by the absence of articles that were acquired independently (e.g., Cutter et al. 2007, Nakhasathien 1987, Scott 1975), even including work published by one of the authors (Sundar 2003, 2005). To avoid subjectivity, we refrained from selectively adding absent publications to our list of results because our knowledge of absent publications would be biased and not comprehensive. Nevertheless, the nearly 1000 publications we found in our search represent the majority of accessible research on storks, though improved methods are likely to incorporate publications that were missed out additionally.

Breeding was the most represented topic in publications, but this was biased by work on the three most studied stork species. The breeding ecology of many stork species remains unstudied (e.g., Gula et al. 2021), even for the rarest species, such as the Storm's Stork and the Milky Stork. Indeed, crucially lacking for most tropical storks were studies that related abundance and basic population parameters to environmental variables, which hampers an ability to understand population dynamics in relation to environmental change. Research in Europe and the USA has exhaustively addressed how variables such as climate and food availability influence the dynamics of Wood Stork and White Stork populations (e.g., Borkhataria et al. 2012, Kamiński et al. 2020, Klassen et al. 2016, Martín et al. 2021, Massemin-Challet et al. 2006). To a much lesser extent, recent work on several Asian species has related breeding success to habitat factors (Kittur and Sundar 2021, Ramachandran et al. 2017, Sundar et al. 2019), but no such work has been published for storks in Africa. Tropical developing countries have different suites of socioecological conditions than temperate developed countries, which means research findings on storks from Europe and the USA should not be extrapolated to inform ecological information, status, or conservation action on tropical storks. For this reason, it is critical to undertake studies on population ecology and habitat associations of storks in the tropics that will inform conservation in the appropriate context.

The number of publications on aspects of habitat and movement was also biased by research on three stork species. Whereas habitat associations or requirements of species such as the Wood Stork (e.g., Beerens et al. 2015, Bryan et al. 2012, Herring et al. 2015) and several Asian species (e.g., Kittur and Sundar 2020, Koju et al. 2019, Sundar 2004, Sundar 2006) have been investigated in detail, publications on the topic of habitat for most other species were not substantive. This represents another significant knowledge gap for storks globally that limits the ability to assess threats and develop conservation plans.

Movement ecology has primarily been studied in stork species with confirmed migratory movements (e.g., Abdim's Stork, *C. abdimii*: Jensen et al. 2006; Oriental Stork: Shimazaki et al. 2004; Yang et al. 2021; White Stork: Chernestov et al. 2004; Rotics et al. 2016; Flack et al. 2016; Black Stork: Bobek et al. 2008; Literák et al. 2017), although the Wood Stork in the USA is a notable exception (Borkhataria et al. 2013, Bryan Jr. et al. 2008, Picardi et al. 2018). More limited telemetry research has also been conducted on the Asian Openbill in Thailand (Ratanakorn et al. 2018), and there has been one postgraduate study on Jabiru (*Jabiru mycteria*) movement in Belize that was not subsequently published and, therefore, not included in our literature search (Figueroa 2005). Besides contributing to understanding habitat use, telemetry may shed light on population connectivity and unknown migration patterns for the remaining species and populations that have not been studied. For example, there is a known migratory population of African Woolly-necked

Storks in central Africa that appears to track rainfall, but these dynamics are only known from seasonal influxes of storks into Botswana, Zambia, and Zimbabwe (Aspinwall 1987). It is possible logistical challenges (e.g., accessing nests or capturing and tagging storks) have been impediments to research on tropical stork movement (Gula et al. 2022b), but we see naivete (i.e., about the lack of scientific work on storks), capacity, and funding as more likely contributors. Combining knowledge of movement with genetics, such as has only been done for the White Stork (Shephard et al. 2013), will enhance the understanding of population dynamics and vulnerability, which is why we suggest these research areas are critically needed for most of the tropical stork species.

Cultural aspects connecting stork species to communities can be a strong impetus for conservation (e.g., Czajkowski et al. 2014). Enhancing sociological aspects of research on storks is critically needed and can potentially improve conservation outcomes. One example is the need to address cultural beliefs about the medicinal properties of Marabou Stork parts in Nigeria, where the species has been extirpated as a breeding species but is still imported and heavily traded (Gula and Barlow 2023, Ringim et al. 2021). One of the relatively few publications that locate conservation strategies in the local culture rather than generic protectionist assumptions is Ringim et al. (2021). The rarity of such thinking in literature must be remedied by involving many more local thinkers and scientists.

Although we did not quantify it, most field studies outside of western countries occurred in protected areas, which may explain assumptions about habitat requirements despite an overall lack of data on the topic. Recent work on several species in the tropics and subtropics has shown that significant populations of several stork species occur in agricultural or human-dominated habitats (e.g., Asian Woolly-necked Storks: Kittur and Sundar 2021; Win et al. 2020; African Woolly-necked Stork: Thabethe 2018; Thabethe and Downs 2018; Black-necked Stork: Sundar

2011; Marabou Stork: Pomeroy and Kibuule 2017; Lesser Adjutants: Koju et al., 2019; Sundar et al. 2019). The Greater Adjutant is also now increasing across agricultural landscapes in the Gangetic floodplains of India, but literature on this species is restricted to journals that are not widely read (Mishra and Mandal 2009). Although 12 species were studied in agricultural or urban areas, most studies outside of south Asia did not investigate how these anthropogenically modified environments influence population ecology. Moreover, the overall lack of research on storks in such anthropogenically modified areas, especially in Africa and South America, suggests that the understanding of stork populations and the threats they face is incomplete. In many regions, such as West Africa, cropland has replaced natural habitats at a significant rate, and urban areas are expanding (CILSS 2016, Güneralp et al. 2020). Thus, it is critical to focus attention on both natural refugia and transformed landscape mosaic habitats where some stork species persist and others have disappeared, and to determine the role land use plays in sustaining regional stork populations (Gula et al. 2022a). We cannot accurately assess status and develop conservation plans for several stork species without doing so. Additionally, given that most Asian stork species use farmlands extensively for both foraging and breeding, using counts from volunteer efforts focusing on wetland site counts to "guesstimate" population sizes of stork species should be discontinued. Such one-time wetland counts do very poorly at detecting resident breeding populations of territorial species such as the Black-necked Stork (Sundar 2005), and likely lead to underestimates of unknown extents for other stork species, especially those that may exhibit significant seasonal movements.

Long-term studies of population ecology have been limited to only a few stork species (e.g., Cuadrado et al. 2016, Frederick et al. 2009, Kamiński et al. 2019). This lacuna represents one of the most important data deficiencies for storks globally because, as long-lived species, long-term research is essential for a proper understanding of stork population dynamics and trends (Clutton-Brock and Sheldon 2010, Genovart et al. 2018). It seems no coincidence that long-term research with high-resolution data on population demographics has been restricted to developed countries in Europe and the USA, as such studies are costly to implement and maintain. The lack of empirical population data on many tropical stork species suggests that scientific evidence has contributed sparingly to their IUCN Red List status assessments. Consequently, it appears that most stork species presently listed as Least Concern have never been the subject of a population study, meaning population sizes and trends have not been scientifically assessed.

Expert advice may have been the most common source for stork status assessments, but for many species, such advice is most commonly given by itinerant or parachuting professionals from developed countries and can be biased to individual locations (e.g., southeast Asia population of the Woolly-necked Storks, as described in Sundar 2020), or can be biased by incorrect assumptions (e.g., the unsuitability of tropical farmlands and urban areas for all stork species as recorded in several Red List species assessments). The change in designation for Asian Woolly-necked Storks also suggest that the process of status assignments is sometimes hurried, does not fully consider the opinions of all the participating scientists, and that there is some lack of transparency of how the information provided online in discussion forums are used to finalise status assessments (Sundar 2020). We suggest that future Red List assessments of storks take a more careful approach where evidence can outweigh assumptions as the reason for assigning or changing statuses, especially since new work in Asia is showcasing major assumptions regarding threats to be incorrect for a number of species (Katuwal et al. 2022, Koju et al. 2019, Sundar and Kittur 2013, Win et al. 2020). Indeed, many stork species have a status almost entirely based on opinions and assumptions and are therefore more suited for a listing akin to Data Deficient or the previous classification as Unknown on the Red List. If for some reason species require to be given a status that is not Data Deficient (e.g., see Butchart and Bird 2010), such assessments should carry an explicit indication that the status is assumed and has great uncertainty. We are aware of the thoughts provided as to why bird species should not be assigned a Data Deficient status (Butchart and Bird 2010). However, as we show with a careful independent assessment of storks, a confident assignment of status in other Red List categories, despite no transparent supporting evidence, is not consistent with IUCN Red List norms for other taxa, and has led researchers to overlook species that should be prioritised for research. Although the Red List is not meant to guide research and conservation priorities (IUCN 2016), it inevitably does within the scientific community, and this will likely not change.

Several species traditionally listed as Near Threatened, Vulnerable, or Endangered are not supported by information on their population ecology, habitat requirements, or present conservation status. For example, Red List assessments for the Black-necked Stork, Greater Adjutant, Lesser Adjutant, Milky Stork, and Painted Stork cite rapid population declines caused by threats such as hunting, habitat loss, and pollution despite no such published scientific information. The Painted Stork assessment even acknowledges the species as one of the most abundant Asian storks but still states rapid decline as the justification for a Near Threatened listing. This is despite increasing evidence in the majority of the Painted Stork's range of its ability to use areas with high human presence, such as cities and multi-cropped farmlands with relatively high breeding success of monitored colonies (Suryawanshi and Sundar 2019, Tiwary and Urfi 2016). It appears possible that assumptions regarding requirements of protected and undisturbed wetlands for the breeding of this species (which may be essential in few countries in south-east Asia where hunting of all animals is rife; Harrison et al. 2016) led to these statements that suggest population declines for the species as a whole. The manner of changing status for the Asian Woolly-necked Stork additionally suggests that both the assignment of confident status and especially changes in these statuses require careful oversight, broader discussion, and greater transparency (Sundar 2020). Despite the increasing trend in stork research in the last two decades, population data for science-based status assessments do not exist for most tropical species, so the changes in Red List status in the early 2000s clearly indicate that science-based evidence is not driving the assessments of these species. At least for storks, and likely for other groups of birds, the current Red List will benefit from having many more species correctly identified as being Data Deficient, or otherwise including an additional detail relating to the poor reliability of the accorded species status, and clearly indicating which assumptions were used relative to available scientific evidence.

2.6 Conclusions

Our systematic review of published evidence on storks showed that the focus on Asian species has grown in the past decade, while the endemic African storks remain severely understudied, even regarding aspects of their basic life histories. Besides focusing on understudied species, future research must go beyond merely life history studies and beyond protected areas to investigate how population parameters are influenced by environmental variables and how movement patterns and genetics are related. These areas of study will provide the most useful information for assessing threats and vulnerabilities of populations. We also showed the need to identify species with deficiencies in data, and the consequent absence of evidence-based status assignments for many species. Highlighting these poorly studied species will allow a specific focus on species that require critical work to uncover their basic ecology. Finally, assuming that storks will do well only in protected habitats is incorrect, given the growing number of species persisting in agricultural and suburban areas. Even the species that are not threatened and that remain understudied have the potential to act as ecological indicators, highlighting the need to avoid research bias against species listed as Least Concern, especially if the status assessment is not based on scientific data. The IUCN Red List remains the most influential and important method for governments and scientists to plan and determine conservation action. Considerable financial resources are directed to institutions and individual scientists based on Red List status assessments. Therefore, strengthening this enterprise's robustness is essential to ensure that conservation resources are correctly directed to species that require the most help. As we demonstrate with storks, the Red List can also help direct resources for research on the most deserving, least understood species.

2.7 Funding

We are grateful to the University of KwaZulu-Natal (ZA) and the National Research Foundation (ZA, Grant 9844) for funding. We thank the U.S. Fulbright programme for supporting Jonah Gula's research in South Africa.

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2.9 Supplementary information

Supplementary information Table S2.1: Summary of breeding success estimates in publications on storks globally. Note: not all authors estimate breeding success rates in the same way. Estimates reported as ranges represent estimates across years or areas, if presented as such.

Species	**Hatching success rate**	**Fledging success rate**	**Fecundity (chicks/nest)**	**Influence of variables investigated?**	**Source**
Asian Openbill	64.2–67.1%	78.2–81.5%	–	✓	Datta and Pal 1993
	45.2–45.7%	41.1–42.2%	2.2–2.4	X	G.V. and Pandav 2007
	91.7–94.9%	84–88%	2.7–2.9	X	Pramanik et al. 2014
	–	–	2.4	✓	Sundar et al. 2019
Abdim’s Stork	–	–	2.6	X	Christensen et al. 2008
	80%	–	2.5	X	Ivande et al. 2012
Oriental Stork	–	65%	1.2	X	Ezaki and Ohsako 2012
	–	–	2.2	X	Xue et al. 2010
White Stork	–	–	0.9–1.6	✓	Balmori 2005
	–	–	0.5–1.5	✓	Baos et al. 2012
	–	–	2.1–4.0	✓	Barbraud et al. 1999
	–	–	0.4–2.8	✓	Belabed et al. 2019
	45.8–61.6%	–	2.2–3.3	✓	Benharzallah et al. 2022
	–	–	0.0–5.0	✓	Bialas et al. 2021
	–	–	1.0–2.6	✓	Biber et al. 2003
	–	–	2.3–2.9	✓	Bouriach et al. 2015

Species	Hatching success rate	Fledging success rate	Fecundity (chicks/nest)	Influence of variables investigated?	Source
White Stork (continued)	–	–	0.7–2.7	✓	Cuadrado et al. 2016
	–	–	1.8	X	Denac 2001
	–	–	1.6–2.5	✓	Denac 2006a
	–	–	1.5–3.0	✓	Denac 2006b
	–	–	1.8–2.5	✓	Djerdali et al. 2016
	–	–	2.1	X	Dorner and Tietze 2015
	–	–	1.0–5.0	✓	Fasolă-Mătăsaru et al. 2018
	–	–	2.1	✓	Fulin et al. 2009
	–	–	1.1–3.2	✓	Göcek et al. 2010
	–	–	1.7–3.1	✓	Gordo et al. 2013
	–	–	1.9–2.9	X	Grishchenko 1999
	–	–	0.9-3.0	✓	Hilgartner et al. 2014
	–	–	2.4–3.1	✓	Jacek 2003
	–	–	0.5–2.6	✓	Janiszewski et al. 2013
	–	–	0.0-6.0	✓	Janiszewski et al. 2014
	–	99%	2.6–3.5	✓	Kaługa et al. 2016
	–	–	2.2–3.5	✓	Kopij 2017
	66–85%	–	2.7–3.2	✓	Kosicki 2010
	–	–	1.6–2.6	X	Kujawa 1994

Species	**Hatching success rate**	**Fledging success rate**	**Fecundity (chicks/nest)**	**Influence of variables investigated?**	**Source**
White Stork (continued)	79%	71%	2.5	✓	Massemin-Challet et al. 2006
	–	–	0.0–3.3	✓	Moritzi et al. 2001
	87.4–97.3%	–	0.9–2.6	X	Profus 1991
	–	–	3.4–4.0	✓	Santopaolo et al. 2013
	–	–	0.7–2.6	✓	Schaub et al. 2004
	–	–	1.4–1.9	✓	Si Bachir et al. 2013
	–	–	2.8	X	Stamkoska et al. 2020
	–	–	0.8–3.0	✓	Tobolka et al. 2013
	69–93%	–	0.6–3.0	✓	Tobolka et al. 2015
	–	–	1.9	✓	Tortosa and Redondo 1992
	–	–	1.7–2.9	✓	Tortosa et al. 2002
	–	–	1.4–3.0	✓	Tryjanowski and Kuźniak 2002
	–	–	1.8–3.6	✓	Tryjanowski et al. 2005
	–	–	0.3–3.5	X	Tryjanowski et al. 2005
	–	–	1.2–3.0	✓	Tryjanowski et al. 2009
	–	–	2.2–5.0	X	Tsachalidis and Papageorgiou 1996
	–	–	2.5	X	Tucakov 2006
	–	–	2.7	✓	Vaitkuvienė and Dagys 2014
	–	–	2.7	X	Vaitkuvienė and Dagys 2015

Species	**Hatching success rate**	**Fledging success rate**	**Fecundity (chicks/nest)**	**Influence of variables investigated?**	**Source**
White Stork (continued)	–	–	2.4	X	Vanzi et al. 1994
	–	–	0.7–0.9	✓	Vergara et al. 2006
	–	–	3.8	X	Yavuz et al. 2012
	–	–	2.0–2.8	X	Zbyryt et al. 2014
Asian Woolly-necked Stork	–	–	1.9	X	Ghimire et al. 2022
	–	–	2.5–3.5	✓	Kittur and Sundar 2021
Maguari Stork	39–67%	33.80%	0.3–0.9	X	González 1998
	51–100%	55.5–100%	1–3	X	Thomas 1984
Black Stork	82–88%	87–91%	2.8–3.1	X	Alexandrou et al. 2016
	–	–	3.6	X	Bela and Anna 2003
	–	–	1.6–2.4	✓	Cano-Alonso and Tellería 2013
	–	–	1.1–2.6	X	Czuchnowski and Profus 2008
	–	–	1.1	X	Konovalov et al. 2019
	–	–	1.9–2.2	X	Tarboton 1982
	–	66–71%	2	X	Treinys et al. 2008
	–	–	2.2–3.1	X	Tucakov et al. 2006
Storm’s Stork	67%	–	1	X	Danielsen et al. 1997
Black-necked Stork	–	–	1.0–1.7	X	Clancy and Ford 2013
	–	–	0.3–2.4	✓	Sundar 2011

Species	**Hatching success rate**	**Fledging success rate**	**Fecundity (chicks/nest)**	**Influence of variables investigated?**	**Source**
Saddle-billed Stork	–	–	2.7	X	Gula et al. 2021
Jabiru	43.80%	–	1.5–2.0	X	Barnhill et al. 2005
	–	47.0–47.6%	0.9–1.0	X	González 1996
Marabou Stork	–	–	0.2–1.4	X	Ehlers Smith et al. 2021
	47%	12%	0.4	X	Monadjem 2005
	–	–	0.5–1.1	✓	Monadjem and Bamford 2009
Lesser Adjutant	–	–	1.1–2.0	X	Chowdhury and Sourav 2012
	57.70%	41.70%	0.8	X	G.V. and Pandav 2007
	–	–	1.6	✓	Sundar et al. 2019
Wood Stork	–	54–71%	1.8–2.1	X	Borkhataria et al. 2008
	–	–	1.4–1.8	✓	Bowerman et al. 2007
	–	–	2.6	✓	Bruant et al. 2020
	–	65–100%	1.3–2.7	✓	Bryan and Robinette 2008
	91–93%	4–84%	0.3–2.2	✓	Coulter and Bryan 1995
	–	–	0.0–2.5	✓	Gaines et al. 2000
	–	30.90%	0.7–1.7	X	González 1999
	–	–	0.2–2.6	X	Griffin et al. 2008
	–	–	2.1–2.7	X	Llanes-Quevedo et al. 2015
	–	–	1.7–2.8	X	Murphy and Coker 2008

Species	**Hatching success rate**	**Fledging success rate**	**Fecundity (chicks/nest)**	**Influence of variables investigated?**	**Source**
Wood Stork (continued)	26–89%	–	0.0–2.7	X	Rodgers and Schwikert 1997
	–	–	0.0–2.4	✓	Rodgers et al. 2008
	–	–	1.2–1.5	✓	Rodgers et al. 2012
Painted Stork	61.90%	65%	1.1	X	Desai 1971
	48.0–50.2%	46.70%	0.5–0.6	X	G.V. and Pandav 2007
	–	–	2.4	X	Suryawanshi and Sundar 2019
	27–65%	–	–	X	Urfi et al. 2007

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CHAPTER 3

Breeding ecology of Africa's only known population of urban Woolly-necked Storks (*Ciconia microscelis*)

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Running header: Urban woollyneck breeding

3.1 Abstract

Historically, the African Woolly-necked Stork (*Ciconia microscelis*) was considered a shy and secretive species that occurred in natural wetlands away from human activity. However, in the past few decades, it has rapidly colonised urban mosaic landscapes in KwaZulu-Natal Province, South Africa. We asked: (1) have reproductive rates contributed to the rapid demographic expansion of the species in urban areas, and (2) what factors influenced measures of breeding success? We monitored 112 nesting attempts during two breeding seasons (2022 and 2023) and described some basic aspects of the Woolly-necked Stork's breeding biology in Africa. Daily rainfall rates positively influenced fledging success, but this relationship was weaker in 2023 when fecundity was half that of 2022 (1.4 fledglings per pair in 2022 versus 0.7 in 2023). There was a negative relationship between the date of egg-laying in a season and fledging success, but the proportion of urban residential area around nests did not affect breeding measures. The potential for relatively high fecundity in some years (e.g., 2022) supports the idea that high reproductive rates contributed to the increase and spread of storks during the process of urban colonisation. The case of the African Woolly-necked Stork in KwaZulu-Natal adds to the growing body of knowledge on the nuances of how wildlife adapt to human-modified landscapes.

Keywords: Ciconiidae, fecundity, fledging, hatching, nesting, South Africa

3.2 Introduction

Across the globe, an increasing number of wildlife species have been found to exploit urban environments with varying degrees of success, especially in mosaic landscapes in developing countries (Downs et al. 2021, Muller et al. 2020, Rodríguez et al. 2021, Shlepr et al. 2023). Urban environments generally have been colonised as a response to the loss of natural habitat (Riley et al. 2021, Tigas et al. 2002) or the creation of favourable habitat features (Downs et al. 2021, Hara et al. 2018, Pomeroy and Kibuule 2017, Rodríguez et al. 2021, Rutz 2008). The process in which wildlife becomes "urbanised" is species-dependent and may take many pathways, but generally follows three stages: arrival, adjustment, and spread (Evans et al. 2010). Unfortunately, a general failure to recognise this urbanisation process has meant that research is often too late to capture the first two stages. Thus, it is the effects of post-spread urban ecology that are studied in most species.

For wildlife that have already spread across an urban habitat matrix, exploitation of urban areas has varying outcomes depending on the species, particularly in birds. Observed consequences of urbanisation for passerines have included reduced immunocapacity and breeding success as well as compromised nestling growth because anthropogenic food that benefits adults is relatively poor quality for developing offspring (Bailly et al. 2016, Catto et al. 2021, de Satgé et al. 2019). The tradeoff of an urban life for some raptors has been increased prey availability and nest sites but decreased breeding success (Boal and Mannan 1999, Muller et al. 2020, Sumasgutner et al. 2014). White Storks (*Ciconia ciconia*) in the Iberian Peninsula have experienced increased breeding success because of accessibility to supplemental feeding sites and landfills (Gilbert et al. 2016, Hilgartner et al. 2014), so much so that many storks no longer migrate, which further improves breeding success by allowing for early egg-laying (Soriano-Redondo et al. 2023). Thus, a one-size-fits-all conclusion cannot be reached when considering how urbanisation affects a diversity of avian species across the globe, especially because responses to urbanisation depend on both environmental and human factors (e.g., attitudes and socio-economics; Evans et al. 2010).

Raptors and passerines are common subjects of urban ecology studies because they have most readily colonised or persisted in urban environments (e.g., Catto et al. 2021, Muller et al. 2020, Shipley et al. 2013). However, research has increasingly shown that different waterbird taxa may exploit resource patches within an urban habitat matrix, too (Evans and Gawlik 2020, Hara et al. 2018, Pais De Faria et al. 2023, Rawal et al. 2021). Until recently, the scant literature on the African Woolly-necked Stork (*C. microscelis*; hereafter, woollyneck) generally described it as shy and easily disturbed, particularly during breeding, and usually uncommon or rare in natural wetlands (Brown et al. 1982, Hancock et al. 1992, Scott 1975). In the 1980s, the total breeding population of woollynecks in South Africa was thought be around 30 pairs (Brooke 1984). However, in the last three decades, woollynecks have rapidly expanded–geographically and demographically–in KwaZulu-Natal Province, South Africa, especially in human-modified areas such as cities and farmlands (Allan 2012, Thabethe 2018). Now woollynecks are common residents of many urban areas in KwaZulu-Natal, where groups of dozens of storks have been observed being supplementally fed at residential homes or taking advantage of human refuse sites (Thabethe and Downs 2018; JG, pers. obs.), thus representing urban exploitation that is unparalleled elsewhere in the species' range. Assessment of the first two stages of urban colonisation by woollynecks can only be post-hoc, but positive public perceptions of these storks have resulted in supplemental feeding and are thought to have influenced the novel urban exploitation (Thabethe and Downs 2018). The establishment of large, suitable nesting trees–primarily exotic–in urban neighbourhoods and gardens (Figure 3.1) also has likely facilitated population expansion in a region that was historically dominated by grassland and largely devoid of suitable nest trees (Thabethe 2018).

Figure 3.1: African Woolly-necked Storks now commonly nest in urban areas of KwaZulu-Natal, South Africa, including in residential gardens and along roads.

According to Evans et al.’s (2010) urbanisation framework, high reproductive rates and high dispersal rates facilitate the third stage, the increase and spread in urban areas. In this study, we set out to investigate how the first factor, reproduction, may have contributed–and may continue to contribute–to the demographic growth of woollynecks in urban KwaZulu-Natal mosaic landscapes in the span of just a few decades. We predicted that urban woollynecks have high nest survival and fecundity, which likely have contributed to the population expansion. What ecological trade-offs woollynecks may face in urbanised KwaZulu-Natal also remain unclear, so we tested what intrinsic and environmental factors influence breeding metrics. In particular, we predicted more residential areas around nests would positively influence breeding success metrics because of the assumed benefit of supplemental feeding. We also predicted that the presence of nest "helpers" (Thabethe et al. 2021) would positively influence breeding success because, theoretically, assistance by additional storks should result in greater nestling provisioning. Because of the omnivorous diet of woollynecks, we predicted increased rainfall would benefit them indirectly through greater abundance of amphibians, reptiles, and invertebrates for food. Although the unique situation of woollynecks in urban KwaZulu-Natal is not representative of other populations across sub-Saharan Africa, ours is the first study on the reproductive ecology of woollynecks in Africa and contributes to the growing understanding of how some wildlife species thrive in urban mosaic landscapes.

3.3 Methods

3.3.1 Study area

We studied the nesting of woollynecks in the municipalities of eThekwini, Msunduzi, Richmond, uMngeni, uMshwathi and uMdoni in KwaZulu-Natal, South Africa, primarily between the cities of Durban (8 m a.s.l.) and Howick (1060 m a.s.l.; Figure 3.2). A subtropical climate characterises this region, but a gradient exists across the study area from the coast to higher elevations inland. The mean annual rainfall in the city of Durban (eThewkini Municipality) is 893 mm, and mean annual minimum and maximum temperatures are 13.7° C (July) and 27° C (February), respectively (https://en.climate-data.org/africa/south-africa/kwazulu-natal/durban-511/). The mean annual rainfall in Howick (uMngeni Municipality) is 1074 mm, and mean annual minimum and maximum temperatures are 4.5° C (July) and 25° C (February), respectively (https://en.climate-data.org/africa/south-africa/kwazulu-natal/howick-27052/).

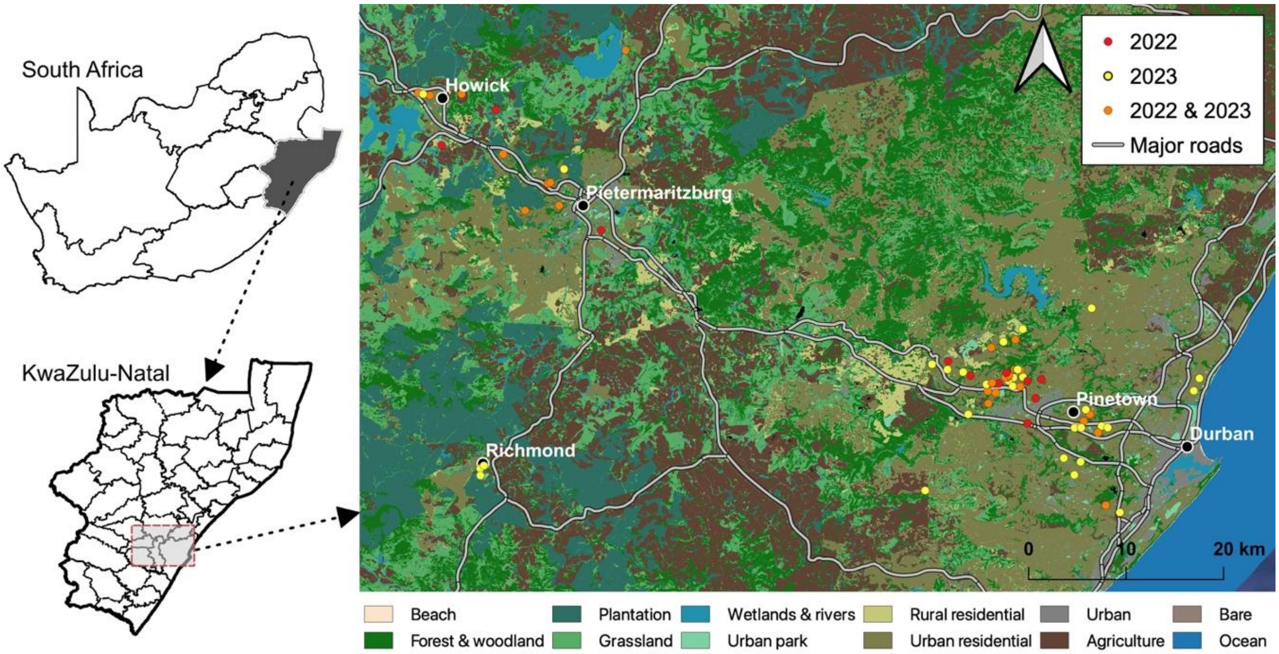

Figure 3.2: A map of African Woolly-necked Stork nests studied in KwaZulu-Natal, South Africa, during two breeding seasons. Note: The map excludes two nests on the south coast in the town of Pennington (2023).

The eThewkini, Msunduzi, and Umdoni municipalities are mosaics of mixed land use, but nests were primarily located in areas of varying levels of urbanisation (commercial and residential use) interspersed by natural and managed green spaces (gardens, parks, conservancies, and nature reserves). The Mkhambathini, Richmond, uMngeni, and uMshwathi municipalities are characterised by greater rural areas and more limited urbanisation than the other municipalities. In the 2022 South African census, population density across the study area varied from 50 people/km^2 in the Richmond Municipality to 1,851 people/km^2 in the eThekwini Municipality (Statistics South Africa 2023).

3.3.2 Nest monitoring

We monitored woollyneck nests from August to March during two breeding seasons (2022 and 2023). We initially located nests via public outreach with local community groups, which subsequently helped create a network of residents who reported nests. We could not systematically survey for nests because of the generally concealed nature of woollyneck nests, inaccessible private property, and saturation of suitable trees across the large study area. We found a smaller number of nests incidentally while travelling in the study area, by following storks with nesting material, and from the movements of storks fitted with telemetry transmitters in a separate study.

Woollyneck nest monitoring began in mid-August when nest-building was underway. We visited nests at least once every two weeks, but usually once per week. After storks were initially observed sitting on a nest, we flew a DJI Mavic Pro drone to count the eggs in the nest, assuming the clutch was complete and no eggs had been lost since laying. We estimated the date of egg laying based on a combination of when storks were first seen sitting on a nest and by backdating from hatch dates, assuming a 30-day incubation period (Scott 1975). Around the projected hatch date, the drone was flown again to confirm the number of eggs that hatched. When nestlings were already present, we approximated their age based on published characteristics (Scott 1975) and experience with known-age nestlings (JG, pers. obs.). We backdated dates for egg laying and hatching if nestlings were found upon initial discovery of a nest. An error of 1–3 days was possible for these date estimates. Rather than using a specific age as a cutoff for fledging, as is common in some studies, we monitored nests until failure or fledging because age at fledging has not been described for woollynecks. Nest checks with the drone were not possible for all nests because of branches around some nests that prevented safe flight.

Given the novelty of this study on woollynecks, we report findings on basic breeding biology, including measures of the timing of breeding, clutch size, and age at fledging. We calculated the hatching rate (proportion of observed eggs that were known to successfully hatch), fledging rate (proportion of eggs known to have successfully hatched that fledged), and fecundity (mean number of fledged nestlings per pair annually, even if zero). We used a chi-square contingency test to determine differences between years for the number of hatched and unhatched eggs and fledged and unfledged chicks. For the estimate of fecundity, only the ultimate number of young fledged from a nest was used, so that for pairs with multiple attempts in a season (defined in this study as eggs laid), the initial failure(s) was not factored into the estimate. We bootstrapped 95% confidence interval estimates of means where appropriate and used these to compare differences between years for clutch size, age at fledging, and fecundity. We used a Fischer’s exact test to determine whether there was variation between years in the size of fledged broods. Finally, we estimated site fidelity as the percentage of nest sites that were used for more than one breeding season. We considered a site to be reused if it was within 50 m in a subsequent year. Because our study was of relatively short duration, we asked members of the public who reported nests used in our study if nesting had occurred prior to our study and incorporated those anecdotes into our estimate of site fidelity. For this reason, we consider the fidelity estimate to be conservative because nest history was not known for all sites before our study.

3.3.3 Nest survival estimation

We estimated woollynecks' nest survival using programme MARK (Dinsmore and Dinsmore 2007, Dinsmore et al. 2002, White and Burnham 1999) for ultimate nest attempts (i.e., for renests, all of which were prompted by failures, we included only the final attempt). To test how survival varied between nesting stages, we estimated daily survival rates for the egg stage, nestling stage, and for the entire nesting period overall. Besides estimating a constant model of nest survival as a null model, we tested a global model that included the effect of year, the presence of nest helpers (0 = no helpers observed, 1 = at least one non-parental stork observed at the nest) and the proportion of residential land cover within a 500 m buffer of the nest as well as a model for each variable individually. Land cover data were derived from the South African National Land Cover 2020 dataset (Department of Agriculture 2020), which had a 20 m resolution. We did not include variables of egg-laying date and rainfall (see below) because of gaps in these data for the nests used in modelling nest survival. We used the average age at fledging to extrapolate the daily survival rate for the nestling period to estimate a total nest survival rate, and combined the 30-day incubation with the average fledging age to estimate an overall nest survival rate. We used the delta method to calculate confidence intervals for the nest survival estimate (Powell 2007).

3.3.4 Breeding success models

We used linear mixed-effects models to test the influence of several intrinsic and environmental variables on breeding success metrics. The breeding parameters modelled were fledging success (0 = no nestlings fledged, 1 = at least one nestling fledged) and fecundity (the number of fledged nestlings per pair). We used logistic mixed models with a logit link and binomial distribution for fledging success. We used a Poisson distribution for the fecundity model because the response variable was a count of nestlings. We included Nest ID as a random factor in all models because some nests were monitored for multiple years and had repeated attempts within a year. Fixed variables related to our hypotheses included the percentage of residential land cover within a 500 m buffer of the nest, the presence of a nest helper (binary), and daily rainfall rate (mm/day) from the date of laying until nest fate (failure or fledging). Because time to fledging varied between nests, we chose to standardise the rainfall variable by weighting it against the period the nest was active, hence the daily rainfall rate rather than total rainfall, which would be incomparable between different nests.

All models were tested to ensure assumptions were met. In the global models, we included an interaction term between year and daily rainfall rate. Daily rainfall data for nests in the suburb of Kloof (eThekwini Municipality) were recorded by Mike Ellis, and daily rainfall data for other nests were sourced from the South African Weather Service. Woollynecks had a prolonged and unsynchronous breeding season, so we additionally included the day of egg laying within a season (day 0 = 1 August) as a fixed variable in our models to account for variable timing of nesting activities among pairs. Finally, we also included year (i.e., breeding season, 2022 or 2023) as a fixed factor to account for interannual differences in breeding success. We used the R packages *lme4* and *MumIn* in R version 4.3.1 (R Core Team 2023) to run models and determine the most parsimonious one using the corrected Akaike Information Criterion (AICc).

3.3.5 Sex ratios and nestling body condition

We used a binomial one-proportion test to test if the woollyneck brood sex ratio at ringing was different from the expected 1:1 ratio. We similarly tested if the sex ratio of fledged nestlings differed from equal. We used linear mixed-effects models and AICc model selection to test the hypothesis that nestlings in areas of greater urbanisation had better body condition. Because data from nestlings were collected at various ages, we estimated a body condition index of nestlings as the residuals from a quadratic regression of body mass (g) regressed against (body size)^2 (Townsend et al. 2018). We defined body size as the first principal component on covariances of two morphological measurements (tarsus and bill lengths); this component explained 95% of the total variation in these measurements. We considered nestlings with positive residuals to be in better condition. We used the percentage of residential land cover within a 500 m buffer of the nest as a fixed factor as well as year and sex as fixed variables. We used the individual nest identity as a random effect using the R packages *lme4* and *MumIn* in R version 4.3.1 (R Core Team 2023).

3.4 Results

3.4.1 Breeding biology

We followed 112 nesting attempts (43 in 2022, 69 in 2023) by woollyneck pairs at 71 unique nests in which eggs were laid. Seven other initially monitored nests were abandoned after initial activity despite some of these pairs staying at nests for up to two months after the first observation at the nest; these were excluded from all analyses. The earliest laying date was 2 August, and the latest was 31 January (n = 84 with known dates). The peak of laying was in the first two weeks of September (Figure 3.3), during which eggs were laid in 42.8% of nests. Hatching occurred between 31 August and 2 March (n = 73 with known date). Fledging occurred between 14 November and 8 March (n = 45 with a known date). Some pairs laid a second (n = 14) or third clutch (n = 1) in the same season if the initial nesting attempt(s) failed, so that 14.3% of nesting attempts were renestings. Only two of these renestings were successful. No pairs reared more than one brood in a season. Woollynecks returned to nest at at least 53.5% of sites.

At least one nest helper was observed at 37% of woollyneck nesting attempts, and several had two helpers. In one case in 2023, a pair of Egyptian Geese (*Alopochen aegyptiaca*) usurped a pair of woollynecks from a nest they had used the previous year, and consequently, they did not nest at the site again. Also, in 2023, Egyptian Geese were observed sitting on two woollyneck nests that had been active in the two weeks prior. At two nest sites, Egyptian Geese nested in old woollyneck nests while the woollyneck pair simultaneously constructed new nests a few branches away.

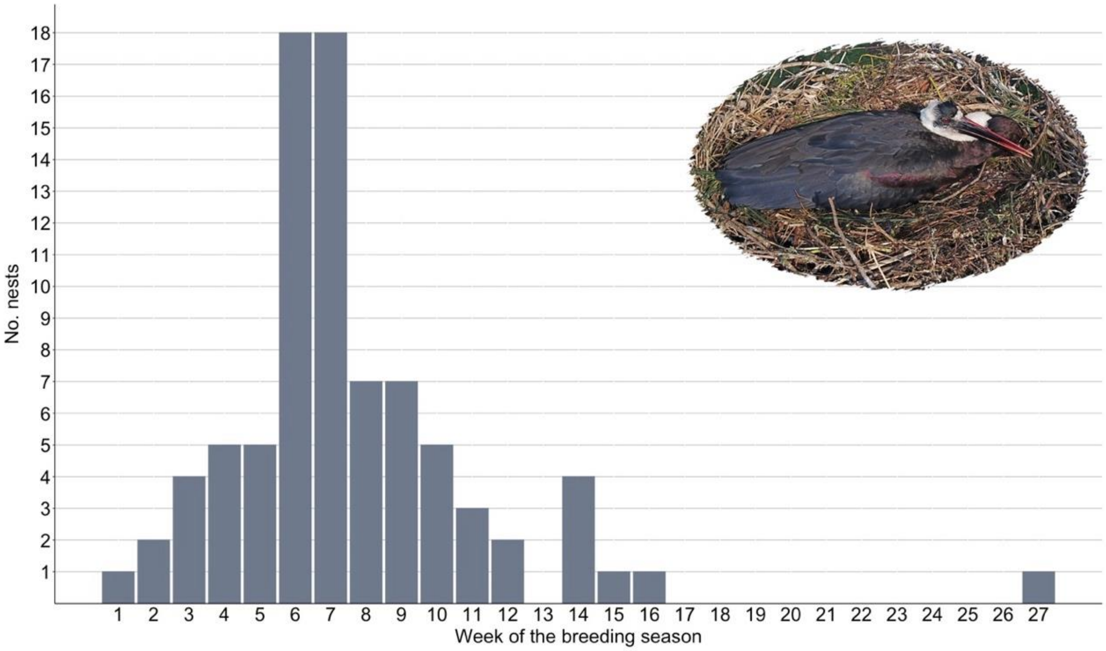

Figure 3.3: Distribution of the timing of African Woolly-necked Stork egg-laying (by week; week 1 = first week of August) for the breeding seasons of 2022 and 2023.

There was no significant difference in woollyneck clutch size between years, and the mean clutch size for both seasons was 3.5 (95% CI: 3.3–3.7, n = 75). The mode clutch size was 4 (range: 2–6, Figure 3.4). The hatching rate was 61.6% (n = 24 nests) in 2022 and 60.6% (n = 35 nests) in

2023, and there was no significant difference between the number of eggs hatched and unhatched between the years ($\chi^2 < 0.001$, $p = 0.99$). The fledging rate was 52.8% (n = 17 nests) in 2022 and 32.4% (n = 24 nests) in 2023, and there was a significant difference between the number of hatched eggs that resulted in fledging and those that did not between the years ($\chi^2 = 4.34$, $p = 0.04$). At least 16.4% of eggs were considered unviable after remaining in the nest without hatching much longer than the incubation period in both seasons. In 2022, of the sample of eggs counted (n = 111), 30.6% resulted in a successfully fledged stork. In 2023, of the sample of eggs counted (n = 150), only 18% resulted in a successfully fledged stork. There was a significant difference in the number of eggs that did and did not result in fledged young between years ($\chi^2 = 4.99$, $p = 0.03$). For both years combined, 23.4% of eggs counted resulted in a successfully fledged stork. There was no significant difference in the age of fledging between years, so the mean for both seasons was 71.5 days (95% CI: 68.6–74, n = 38, range: 56–94). Fecundity differed by year, with 1.4 nestlings fledged per pair (95% CI: 1.1–1.8, n = 37) in 2022 and 0.7 nestlings per pair (95% CI: 0.5–1.0, n = 59). In both years, the mode fecundity was zero. However, in 2022, 51.4% of nests fledged two or three nestlings, while in 2023, only 20.3% fledged two or three. There was a significant difference between the size of fledged broods between years ($p = 0.05$), which was likely caused by more nests fledging just one chick in 2023.

3.4.2 Nest survival and breeding success

For both the woollyneck egg and nestling stages, the constant (null) models ranked highest in AIC model selection. The survival rate of woollyneck nests during the egg stage was 83.3% (95% CI: 81.5–84%). The survival rate during the nestling stage was 65.2% (95% CI: 59.7–62.4%). For overall nest survival, the best model featured only year as a variable, indicating lower survival in

2023. The overall nest survival rate from egg-laying to fledging for both years was 56.5% (95% CI: 54.7–56.9%).

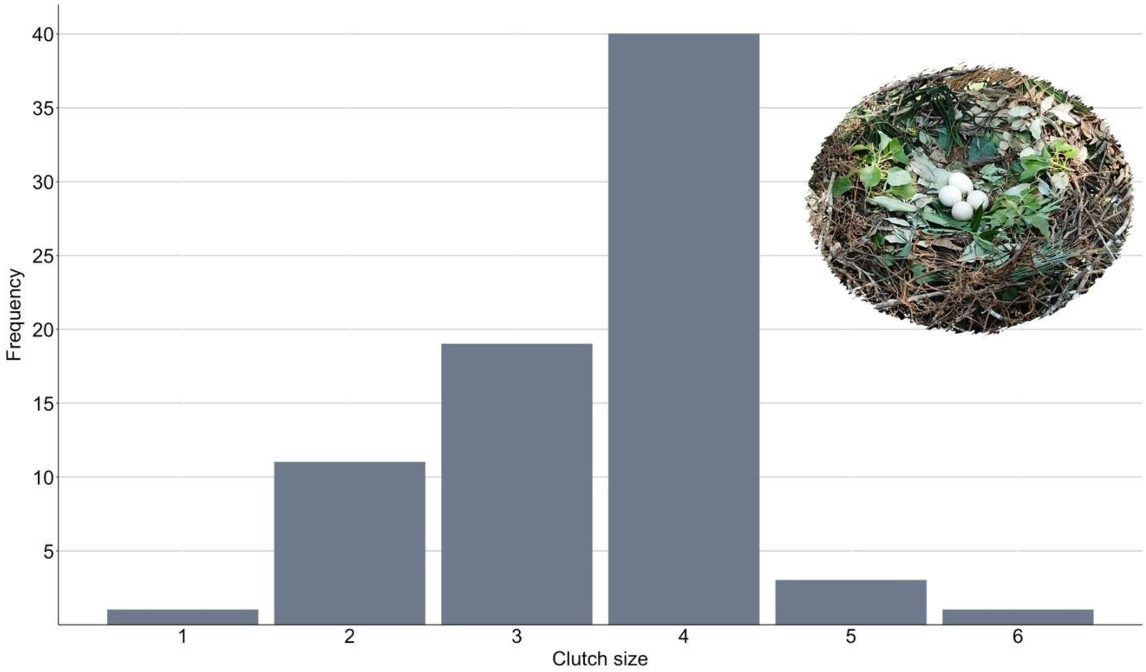

Figure 3.4: Distribution of clutch size in 75 nesting attempts of African Woolly-necked Storks in the breeding seasons of 2022 and 2023.

The global model of woollyneck fledging success was the most parsimonious, in which the date of egg-laying, daily rain rate, and the interaction between year and daily rain rate had significant effects (Table 3.1). The model explained 60.7% of the variation in the data, 44.8% of which was attributed to fixed effects. Chances of successfully fledging at least one nestling decreased as the date of egg-laying advanced in a season (Figure 3.5). Daily rainfall rate positively affected chances of fledging success, but this relationship was weaker in 2023 than in 2022 (Figure 3.5). For fecundity, the most parsimonious model included only year, in which fecundity in 2023 was nearly half that of 2022 (Table 3.2). The model explained relatively little variation in the data (21.7%), of which year only explained 8%.

Table 3.1: Summary showing (a) model selection table for fledging success models, and (b) parameter estimates for the top model. Parameters with a significant effect ($\boldsymbol{\alpha}$ = 0.05) are in bold.

(a) Response: fledging success (binomial) (n = 74 nesting attempts)

Model	AIC$_c$	ΔAIC$_c$	$\acute{\omega}_i$
Lay date + Percent residential + Help + Rain rate*Year	96.8	0.00	0.89
Year	103.2	6.34	0.04
Lay date	103.9	7.06	0.03
Null	104.4	7.61	0.02
Help	105.6	8.80	0.01
Rain rate	105.9	9.04	0.01
Percent residential	105.9	9.10	<0.00

(b) Top model: Lay date + Percent residential + Help + Rain rate*Year

Parameter	Estimate ± SE	*z*-value	*p*
Intercept	-3.07 ± 2.44	-1.26	0.21
Lay date	-0.05 ± 0.02	-2.52	**0.01**
Percent residential	-1.54 ± 1.78	-0.87	0.39
Help	-0.65 ± 0.80	-0.82	0.41
Rain rate	2.11 ± 0.90	2.35	**0.02**
Year (2023)	5.52 ± 2.97	1.86	0.06
Rain rate:Year (2023)	-1.87 ± 0.85	-2.21	**0.03**

Table 3.2: Summary showing (a) model selection table for fecundity models; and (b) parameter estimates for the top model. Parameters with a significant effect (**α** = 0.05) are in bold.

(a) Response: fecundity (number of fledged young per pair) (n = 74 nesting attempts)

Model	AIC$_c$	ΔAIC$_c$	$\acute{\omega}_i$
Year	199.1	0.00	0.64
Lay day + Percent residential + Help + Rain rate*Year	202.0	2.93	0.15
Lay day	203.8	4.75	0.06
Null	203.9	4.85	0.06
Help	204.2	5.12	0.05
Percent residential	205.8	6.79	0.02
Rain rate	206.1	7.00	0.02

(b) Top model: Year

Parameter	Estimate ± SE	*z*-value	*p*
Intercept	0.25 ± 0.20	1.27	0.20
Year (2023)	-0.65 ± 0.25	-2.66	**<0.01**

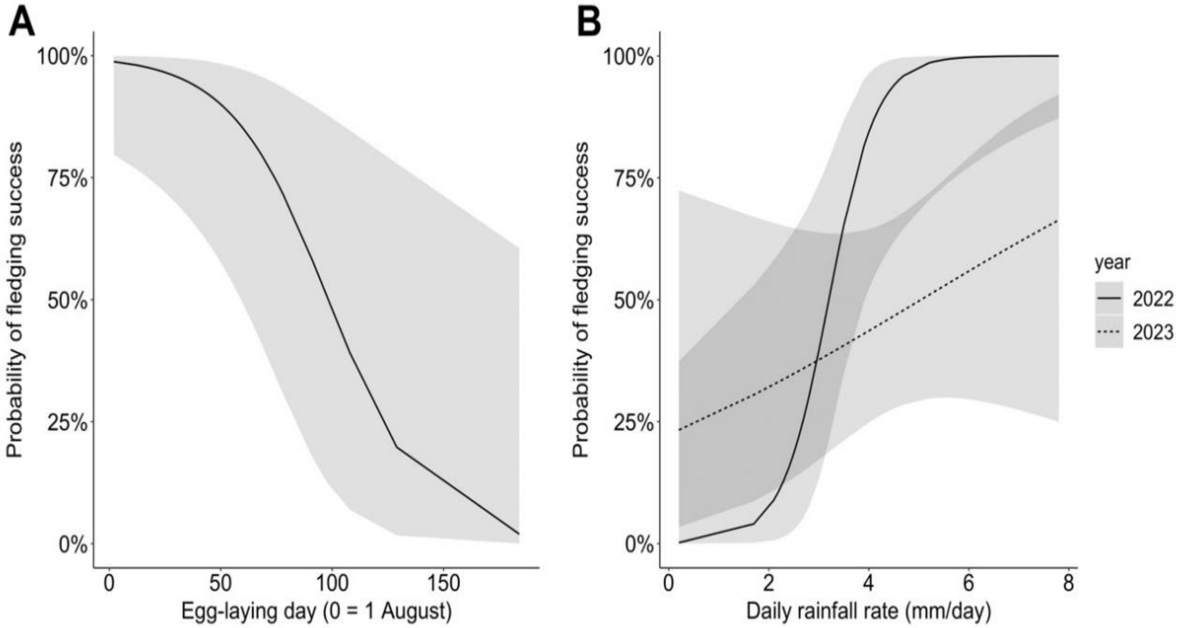

Figure 3.5: The modelled relationship between chances of African Woolly-necked Stork fledging success and (A) egg-laying day in a season and (B) interaction between year and daily rainfall rate.

3.4.3 Nestlings

We colour-ringed and collected data from 76 nestling woollynecks from 38 nesting attempts at 30 nest sites. We collected blood samples and morphometric data from an additional two freshly-dead nestlings that were siblings of colour-ringed nestlings. The brood sex ratio at the time of ringing was not significantly different from the expected equal ratio (51% male: 49% female; $n = 77$ nestlings from 35 broods; $p = 1$). The sex ratio of nestlings that fledged was also not significantly different from the expected equal ratio (49% male: 51% female; $n = 59$ nestlings from 35 broods; $p = 1$). The best model of nestling body condition was the complete model, in which body condition was not affected by the percentage of residential land cover around the nest nor year (Table 3.3). Sex influenced body condition, with males having significantly greater body condition. However, the majority of the variation in the data (conditional $r^2 = 0.63$) was explained by the random effect of nest identity.

Table 3.3: Summary showing (a) model selection table for body condition models, and (b) parameter estimates for the top model. Parameters with a significant effect ($\boldsymbol{\alpha} = 0.05$) are in bold.

(a) Response: body condition (n = 74 nestlings)			
Model	AIC_c	ΔAIC_c	$\acute{\omega}_i$
Percent residential + year + sex	890.3	0.00	0.999
Null	905.5	15.18	0.001
Sex	914.3	24.05	<0.000
Percent residential	916.6	26.29	<0.000
Year	923.5	33.21	<0.000
(b) Top model: Year			
Parameter	Estimate ± SE	*t*-value	*p*
Intercept	-60.87	-0.66	0.52
Percent residential	24.88	0.22	0.83
Year (2023)	3.57	0.12	0.90
Sex (M)	81.52	3.49	**0.001**

3.5 Discussion

KwaZulu-Natal, South Africa, is the only recorded place in Africa where woollynecks have colonised urban areas, much in contrast to historical descriptions of their shy and secretive behaviour (Brown et al. 1982, Hancock et al. 1992). Also, in contrast with the historical record of only two known nests in secluded swamp forest on the north coast of KwaZulu-Natal (Clancey

1964), we recorded dozens of nesting pairs across KwaZulu-Natal. Further, our study was the first to investigate the breeding ecology of urban woollynecks, detailing basic reproductive parameters and factors influencing breeding success.

Overall, the breeding outcomes in 2023 were much poorer than in 2022, including fecundity, which was half of what it was in 2022. The hatching rate of woollynecks in our study was the only metric that was similar between years, and the nest survival rate during the incubation period was relatively high. This finding unsurprisingly suggests that what occurs during the nestling period most determines the ultimate fate of a nesting attempt.

We expected a benefit of anthropogenic supplemental feeding, but contrary to our prediction, the proportion of residential land cover around nests did not influence woollyneck breeding success. As predicted, increased daily rainfall positively influenced woollyneck breeding success in both years, although this effect was weaker in 2023. This difference between years was likely a consequence of more intense storms (high rainfall and wind) between September and December 2023 than in 2022. We could not account for this factor in our modelling approach because of the limitations of the data, but nearly half of the nest failures in 2023 occurred on or within a day of a windy storm with more than 20 mm of rain. In several of these cases, entire nests with nestlings were blown out of a nest tree.

The positive effect of daily rainfall on the breeding success of woollynecks may indicate the importance of natural prey (e.g., amphibians) for provisioning young because these animals increase in abundance with higher rainfall. The majority (67%) of food items provided to woollyneck nestlings in our study area were natural prey (Thabethe et al. 2021), which supports the role of rainfall influencing natural prey abundance during nesting. On the other hand, the negative relationship between breeding success and egg-laying date suggests that increasing total rainfall may negatively influence breeding success because rainfall in KwaZulu-Natal generally increases as the breeding season progresses (M. Ellis, unpub. data). This may reflect an increasing number of storms in early summer that can lead to nest failures caused by exposure (especially of younger nestlings) or nests collapsing, as has been found for African Crowned Eagles (*Stephanoaetus coronatus*) in our study area (Muller et al. 2020)

The lack of a relationship between the residential area around woollyneck nests and their breeding success in KwaZulu-Natal, as well as the high proportion of natural food provisioned to nestlings (Thabethe et al. 2021), does not necessarily negate the benefit of anthropogenic food in urban areas. Although our study did not include a year of below-average rainfall, supplemental feeding could be important in years when natural food for provisioning young is low. Most likely, anthropogenic food is a readily available and stable resource for woollyneck adults, but it may not strongly influence the survival of nestlings. Adult Red-winged Starlings (*Onychognathus morio*) in Cape Town, South Africa, benefited from a large proportion of anthropogenic food in their diets, but the health of nestlings provisioned with the same food was negatively affected. While this finding for adult starlings may accord with the likely situation for adult woollynecks in urban KwaZulu-Natal, the negative effect on woollyneck nestlings does not seem apparent despite there being only 11% more anthropogenic food in the diet of starling nestlings than woollyneck nestlings (Thabethe et al. 2021). The difference, in effect, could relate to the content of the anthropogenic food items fed to each species. Starling nestlings were fed a diet high in carbohydrates and low in protein, leading to nutritional deficiencies (Catto et al. 2021). The majority of surveyed residents in urban KwaZulu-Natal fed woollynecks meat (63.4%) and cheese (21%; Thabethe et al., 2021), which are protein-rich and fat-rich foods that may meet the nutritional requirements of developing nestlings (Seress and Liker 2015). Additionally, this protein-rich and fat-rich diet of adult woollynecks during the pre-laying period could positively affect the chances of nestling survival via improved egg quality (Meyrier et al. 2017, Reynolds et al. 2003). A more detailed study on woollyneck physiology and nestling health is required to understand the true relationship between supplemental feeding and nestling health and survival, as well as how adult diet plays a role. An equally possible explanation of our findings is that the residential land cover variable did not accurately reflect aspects of supplemental feeding (i.e., prevalence, food abundance, and food quality), but we had no other data to address this aspect of urban woollyneck ecology.

To our knowledge, urban woollynecks are the only storks recorded to engage in what appears to be cooperative breeding, as initially described by Thabethe et al. (2021; although see Griesser and Suzuki (2016), who reference White Storks cooperatively breeding without any source of this information). Because of the lack of study on a woollyneck population in natural habitats, we do not know if this behaviour is unique to urban KwaZulu-Natal. Our prediction that nest helpers would improve the chances of fledging success was not supported. It is unknown if nest helpers are related to the breeding pair and if they actually assist in raising young, but filling these important knowledge gaps would shed light on our unexpected results. The lack of a benefit to breeding success in the presence of nest helpers is not unheard of in other birds (Caffrey 2000, Legge 2000, Manica and Marini 2012). However, even if helper woollynecks do not contribute to provisioning nestlings, one would expect the benefit of additional nest defence against predators (Koenig et al. 2019, Valencia et al. 2006) would still contribute to increased chances of success. Although it was not possible to determine the causes of nest failure in most cases, some of our anecdotal observations suggest helpers may accidentally knock nest contents out of the nest. With no apparent benefit to breeding outcomes, and this potential negative effect, it is possible that cooperative breeding in urban woollynecks is actually maladaptive. A detailed study on this interesting aspect of urban woollyneck ecology is required for further conclusions, though.

The concealed nature of woollyneck nests combined with limitations of private land access resulted in few nests found in truly rural areas. Ideally, a study would compare breeding outcomes of rural and urban nests in ways that go beyond simply including our residential land cover variable. Many studies have demonstrated apparent benefits to an urban lifestyle versus rural, including larger body size (Auman et al. 2008), earlier laying dates (Rylander et al. 2024), and enhanced foraging efficiency (McKinney and Raposa 2013), but the overall trend is that of lower breeding productivity in urban areas (Chamberlain et al. 2009). Ours was the first study on the breeding ecology of woollynecks in Africa, so there is no comparison to make with other environments outside the human-modified landscape of KwaZulu-Natal. Nevertheless, the breeding parameters we found were within the range of those reported from studies of other stork species globally in both temperate and tropical regions (see Appendix B in Gula et al. 2023). Breeding success of Asian Woolly-necked Storks (*C. episcopus*) in an agricultural area of northern India was over twice as high (Kittur and Sundar 2021) as that observed in urban KwaZulu-Natal, but our lack of nests in similar areas of KwaZulu-Natal has precluded meaningful comparison.

There do not appear to be particularly apparent ecological tradeoffs of urban breeding for woollynecks in KwaZulu-Natal, as has been found for other urban wildlife in our study area (Muller et al. 2020, Pillay and Downs 2024). It is difficult to determine which of our two study years, each with very different breeding outcomes, is considered average for woollynecks, but further years of study will answer this question. Nevertheless, if an overall nest survival rate of over 50%, as we found, is maintained across years, this provides a partial explanation to our question of how KwaZulu-Natal’s woollyneck population could have demographically expanded so rapidly in a few decades. Additionally, if most pairs fledge two or three young, as was the case in 2022, this represents fairly high recruitment into the urban population. These findings seem to align with Evan et al.'s (2010) framework of urbanisation, namely that high reproductive rates facilitate geographic spread in urban areas, the third stage of urbanisation. In this third stage, woollynecks could continue to increase in abundance (Downs et al. 2021), assuming suitable nest trees (i.e., primarily exotic species) remain abundant. What factors may limit continued spread into areas that are yet to be colonised remains to be seen, but clearly some components of an urban lifestyle have benefited woollynecks in Kwa-Zulu-Natal and have contributed to their growing abundance and distribution.

Other stork species, particularly White Storks and Marabou Storks (*Leptoptilos crumenifer*), have become reliant on anthropogenic food sites (e.g., landfills and abattoirs), and this reliable food source has changed the population ecology of entire regions (Gilbert et al. 2016, Marcelino et al. 2023, Pomeroy and Kibuule 2017, Pomeroy and Kibuule 2021). Clearly, woollynecks in KwaZulu-Natal have followed this trend, too, aided by beneficial characteristics of residential areas, such as supplemental feeding and abundant nest sites. Besides contributing to the growing understanding of this unprecedented ecology of woollynecks in Africa, our study enhanced the understanding of the general life history of woollynecks. We also added to the expanding knowledge of how human-modified environments can support waterbird populations and confer benefits (Hara et al. 2018, Kittur and Sundar 2021, Mehta et al. 2024, Shlepr et al. 2023), contrary to the conventional and unnuanced narrative that urbanisation negatively affects wildlife.

3.6 Acknowledgements

We thank the University of KwaZulu-Natal and the National Research Foundation (ZA, Grant 9844) for funding, as well as the Ford Wildlife Foundation (ZA) for vehicle support. We thank the U.S. Fulbright programme for supporting Jonah's research. Thanks to Themba Manzini for climbing to stork nests for us, to the many residents who allowed access to nests or allowed us to capture storks at their homes.

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CHAPTER 4

Natal dispersal of immature African Woolly-necked Storks (*Ciconia microscelis*) in an urban-colonised area of South Africa

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Running header: Woolly-necked Stork natal dispersal

4.1 Abstract

Natal dispersal can play an important role in the expansion of wildlife populations, especially at range peripheries. The African Woolly-necked Stork (*Ciconia microscelis*) population in KwaZulu-Natal, South Africa, has geographically and demographically expanded significantly in the past few decades. We investigated the dispersal of immature storks using high-resolution telemetry data and low-resolution colour-ring mark-resight from August 2022 to November 2024. We tagged four immature females using global positioning system (GPS) transmitters and colour-ringed 76 nestlings. The GPS-tagged immature storks moved across large areas during their dispersal period and reduced the size of their occurrence distributions as they aged. The farthest a GPS-tagged stork moved from its natal nest site was 220 km. Colour-ringed immatures were resighted an average of 26.5 ± 16.9 (SD) km from their natal site, and as far as 98 km in one case. For a bird of its size, these dispersal distances are not unexpected, but they provide insight into how KwaZulu-Natal's stork population could have expanded geographically in such a short period of time. What remains to be seen is if the population will continue to expand southward and inland with such dispersal movements.

Keywords: Ciconiidae, dispersal, indepdence, movement, roosting

4.2 Introduction

Natal dispersal, defined as the movement between an animal's natal area and its first breeding area (Howard 1960), is a fundamental component of population ecology that influences population demographics, genetics, and social evolution (Johnson et al. 2009, Pasinelli and Walters 2002, Vandergast et al. 2022). Dispersal plays a significant role in the expansion of populations, such as at the periphery of geographic ranges (Courant et al. 2019, Gaston 2003) or into novel habitats (Evans et al. 2010). Immature animals most often exhibit exploratory behaviour during the process of natal dispersal (Debeffe et al. 2013, Ferrer 1993), which means they are most likely to encounter novel suitable habitats and initiate the early stages of population expansion (Evans et al. 2010).

As many parts of the world become increasingly urbanised, more wildlife populations encounter novel human-made environments. Numerous studies have demonstrated the success of some bird species persisting in or colonising urban habitats (Downs et al. 2021, Duckworth et al. 2010, Mehta et al. 2024, Stout and Rosenfield 2010). The colonisation of the urban mosaic landscape is predicated on three simple stages: arrival, adjustment, and spread (Evans et al. 2010). This colonisation process is determined by a balance between dispersal distances, survival, and the number of dispersers, which depend on habitat and dispersal behaviour (Bocedi et al. 2014). Immature animals are generally the most dispersive individuals in a population because of their exploratory behaviour post-independence (Debeffe et al. 2013, Ferrer 1993), which means this age class may play a disproportionate role in facilitating population expansion into unoccupied areas, such as urban landscapes. This effect may be enhanced at range edges, where dispersal rates and distances may be highest (Courant et al. 2019, Lindström et al. 2013).

African Woolly-necked Storks (*Ciconia microscelis*; hereafter, 'woollynecks') in South Africa's KwaZulu-Natal Province have experienced a significant geographic and demographic expansion in the past three decades, particularly into urban areas (Thabethe 2018). Previously, woollynecks were scarcely observed south of the Mlalazi River near the town of Mtunzini (Clancey 1964, Cyrus and Robson 1980). However, to date they have been regularly recorded as far south as the Eastern Cape Province border, where breeding has also been recorded (eBird 2024, SABAP2 2024).

The expansion of KwaZulu-Natal's woollynecks is unprecedented for the species in Africa and is noteworthy in several regards. Firstly, woollynecks were conventionally described as shy and secretive (Brown et al. 1982, Hancock et al. 1992), yet now they are commonly habituated in residential areas and receive supplemental food from people in urban backyards (Thabethe and Downs 2018). Secondly, the near-200-km southward expansion of a breeding population of woollynecks suggests high reproductive rates and/or dispersal, which is representative of the wildlife successfully colonising urban mosaic landscapes (Evans et al. 2010), including those with natural or managed (e.g., gardens, parks, golf courses, etc.) green spaces (Downs et al., 2021). Finally, the expanded woollyneck population remains at the southern edge of the species' geographic range. Most wildlife populations at range peripheries are small (Bahn et al. 2006), but the abundance of anthropogenic and natural food in the human-modified, mosaic landscape of KwaZulu-Natal seems to have produced ideal conditions for explosive population growth. All these aspects make the woollyneck expansion an interesting phenomenon to study.

We aimed to explore how dispersal, one of the main drivers of urban wildlife population spread, may have helped facilitate the expansion of woollynecks in KwaZulu-Natal. In particular, we focused on the natal dispersal of immature storks because of the likelihood that this age cohort played a pivotal role as pioneers on the colonisation front. In the absence of data on age at first breeding for woollynecks, we use the term 'dispersal' to simply refer to movement away from the natal area. Essentially, our treatment is more indicative of dispersal potential, which we consider representative of how immatures could ultimately move to their first breeding site.

We used global positioning system (GPS) telemetry and colour-ringing to describe dispersal movement of immature woollynecks up to two years of age. Although somewhat contrary to the idea that resource abundance (i.e., residential areas with supplemental feeding) promotes philopatry (Forero et al. 2002), we predicted that immature woollynecks would disperse away from the natal area at distances farther than their parents move from the nest because this seems one of the most plausible explanations for colonisation in South Africa. While understanding what precipitated the expansion of woollynecks from natural habitats in Zululand will likely always remain a mystery, we expect our hypothesised dispersal behaviour contributed to the expansion and may continue to do so. Besides being the first study to describe such aspects of the natural history of woollynecks, our findings also contribute to the growing understanding of how wildlife becomes urbanised at a population level.

4.3 Methods

4.3.1 Study area

We studied the biology of immature woollynecks in the municipalities of eThekwini, Mkhambathini, Msunduzi, Richmond, uMngeni, uMshwathi and uMdoni, but primarily between the cities of Durban (8 m a.s.l.) and Howick (1060 m a.s.l.). This region is characterised by a subtropical climate, but a gradient exists across the study area from the coast to higher elevations inland. The mean annual rainfall in the city of Durban (eThewkini Municipality) is 893 mm, and mean annual minimum and maximum temperatures are 13.7° C (July) and 27° C (February), respectively (https://en.climate-data.org/africa/south-africa/kwazulu-natal/durban-511/). Mean annual rainfall in Howick (uMngeni Municipality) is 1074 mm, and mean annual minimum and maximum temperatures are 4.5° C (July) and 25° C (February), respectively (https://en.climate-data.org/africa/south-africa/kwazulu-natal/howick-27052/). The eThewkini, Msunduzi, and Umdoni municipalities are mosaics of mixed land use, but nests were primarily located in areas of varying levels of urbanisation (commercial and residential use) interspersed by natural and managed green spaces (gardens, parks, conservancies, and nature reserves). The Mkhambathini, Richmond, uMngeni, and uMshwathi Municipalities are characterised by greater rural area and more limited urbanisation than the other municipalities. Population density across the study area in 2022 varied from 50 people/km^2 in the Richmond Municipality to 1,851 people/km^2 in the eThekwini Municipality (Statistics South Africa 2023).

4.3.2 Nestling colour-ringing

Between 25 and 45 days after hatching, we accessed nestling woollynecks in nests across the study area (Chapter 3) with the help of a professional tree climber from October to November 2022 and September to December 2023. The climber lowered nestlings in a cloth bag to the ground, where we fitted alpha-numeric colour-rings on their tibias and took morphological measurements. We collected a blood sample from the brachial vein on FTA® paper from each captured woollyneck, and subsequently extracted DNA using an E.Z.N.A.® extraction kit (Omega Bio-tek, Inc., Georgia, USA), following the manufacturer's protocols. We sent samples to a commercial laboratory for molecular sexing (Molecular Diagnostics Services Pty Ltd, Westville, South Africa). Nestlings were returned to the nest within 20 min of being removed.

4.3.3 Movement analyses

We used telemetry and colour-ring resightings and recoveries to describe the movement of immature woollynecks, including occurrence distributions and potential dispersal distances. Between August 2022 and August 2023, we captured fledged immature woollynecks in residential gardens or business parking lots using a baited net walk-in trap or a baited custom foot-noose trap made of a garden trellis and monofilament fishing line. One immature woollyneck was fitted with a transmitter after being rehabilitated from an injury. We attached GPS/GSM telemetry transmitters (Sigfox 0G Technology, Randburg, South Africa, 85 g, or Druid Technology, Shenzhen, China, 28 g) to captured woollynecks using a Teflon® or Spectra® harness in a backpack style (Mielke and Handschuh 2018), and programmed them to record one location every 30 min during day and night. Two captured woollynecks were colour-ringed as nestlings, so their exact ages were known. For others, we identified juveniles (<1 year old) by a black-streaked forehead and brownish-red irises, which only turn completely white and red, respectively, around one year of age (Figure 4.1; JG, pers. obs.). Similar to woollyneck nestlings, we collected blood samples for molecular sexing. We also measured the body mass of each captured woollyneck and fit the two not ringed as nestlings with unique alpha-numeric colour-rings before releasing them within 20 min of capture.

Because woollynecks are diurnal, after filtering erroneous GPS locations, we limited spatial use analyses to diurnal GPS locations from immature woollynecks by filtering data to the period from 30 min before sunrise to 30 min after sunrise on the online platform *MoveApps* (Kölzsch et al. 2024) using the "Upload File from Local System" and "Filter/Annotate Day or Night" apps (Kölzsch 2024, Kölzsch and Scharf 2023). We assessed the range residency of woollynecks using variograms in R version 4.3.1 (R Core Team 2023). None of the immature woollynecks were range residents, so we used dynamic Brownian bridge movement models (dBBMM) to estimate occurrence distributions (Kranstauber et al. 2012) on *MoveApps* using the Occurrence Distribution (Dynamic Brownian Bridge) app (Kölzsch and Scharf 2024). Because our tracking period included dispersal movements, we were interested in how occurrence distributions might change from the first year of independence to the second, when presumably an individual has begun to settle in an area after dispersal exploration. Therefore, we split the telemetry data into two periods for three individuals we tracked for over one year. We only tracked the fourth individual for one year. Finally, we calculated Euclidean distances between the natal area and the farthest GPS location during tracking to measure dispersal potential. We also calculated this distance between the natal area and the centroid of the 95% dBMM occurrence distribution in the second year of tracking, as we expect this is most representative of actual dispersal between the natal area and approximate home range establishment during maturity.

Figure 4.1: A comparison of (A) juvenile (<1 year old) and (B) adult African Woolly-necked Storks. Juveniles have white foreheads streaked with black, whereas adults have completely white foreheads. The irises change from brownish-red to red near one year old. The juvenile pictured in (A) is near to one-year-old.

Between December 2022 and November 2024, we monthly solicited resightings of colour-ringed woollynecks on Facebook® and WhatsApp® community groups as well as during irregular public presentations. During this period, JG also regularly visited areas where woollynecks were known to congregate (from public reports and telemetry data) to search for colour-ringed individuals. For all resightings, we recorded the ring code, location, and date. From both telemetry and colour-ring resighting data, we determined minimum age at independence (when they were observed ≥3 km from their natal nest and without parents) and minimum Euclidean distances to inform about potential dispersal distances. For colour-ring resighting distances, we only considered observations ≥3 km from their natal nest based on the distances breeding adults moved from the nest (Chapter 5). Resightings within 3 km of the nest were excluded because they were largely during the post-fledging period when juveniles were still with their parents. Additionally, by definition, locations within this area would not be considered natal dispersal.

4.3.4 Nocturnal roost site fidelity

To determine nocturnal roost site locations, we filtered telemetry data to the period from 30 min after sunset to 30 min before sunrise on the online platform *MoveApps* (Kölzsch et al. 2024) using the "Upload File from Local System" and "Filter/Annotate Day or Night" apps (Kölzsch 2024, Kölzsch and Scharf 2023). We excluded solitary GPS locations from nocturnal roost transition movements (see Results), so only clustered roosting data remained. We generated centroids of nocturnal GPS location clusters to identify distinct roost sites for each individual woollyneck. We defined a roost site as anything within a 30 m buffer of the centroids, and calculated the number of unique nights that each stork spent at a given roost site. We classified roost sites into land use categories and estimated roost site fidelity as the number of nights used divided by the total number of nights an individual was recorded roosting. We performed spatial analyses of nocturnal roosts in QGIS 3.18 (QGIS Development Team 2021).

4.4 Results

4.4.1 Movement

We collected 82,151 GPS locations ($\bar{x}$ = 20,538 per individual) from four immature, female woollynecks between August 2022 and August 2024 (Figure 4.2). All four woollynecks were less than one-year-old when captured, and the duration each was tracked ranged from 370–738 days. The sizes of the dBBMM occurrence distributions varied greatly between individuals (Table 4.1). For the three females that were tracked over one year, each reduced the size of their distribution in the second year of tracking, although this reduction was small for the Forest Hills female. For the Kloof and Sibaya females, the distribution in the second year was less than half the size of that in the first year. The Mt. Edgecombe female, who was only tracked for one year, had the largest distribution at 299.32 km^2.

Table 4.1: Body mass, tracking duration, and dBBMM occurrence distribution (OD) sizes for immature, female African Woolly-necked Storks in KwaZulu-Natal, South Africa, at different ages.

Individual	Age (months)*	Body mass (g)	Tracking duration (days)	95% OD (km^2)	50% OD (km^2)	Dispersal distance (km)
Forest Hills	10–22	1,770	365	104.05	6.54	52
	23–34		373	97.43	4.32	
Kloof	11–22	2,000	365	68.45	0.54	0.48
	23–34		335	30.7	0.66	
Mt. Edgecombe	11–23	1,250	370	299.32	0.48	220
Sibaya	6–18	-	365	205.89	2.24	82
	19–23		148	83.37	0.91	

*approximated for Forest Hills and Kloof females based on plumage and average hatching time in a breeding season

The Forest Hills female dispersed from her natal area in October 2022 and never returned. This movement coincided with the timing of egg-laying by adults at what we presumed was her natal nest. The farthest GPS location from her centre of activity in the natal area was 52 km, and the Euclidean distance from this activity centre to the centroid of her 95% dBBMM occurrence distribution in her second year was 39 km. Other than two days of exploratory movements inland and down the coast, the Kloof female largely remained within her natal area and participated in nesting with her parents. We observed her incubating at her natal nest site during the 2023 and 2024 nesting seasons. Whether she laid the eggs or was participating as a 'helper' (Thabethe et al. 2021) was unknown. The farthest GPS location from her natal nest was 67 km, and the Euclidean distance from her natal nest to the centroid of her 95% dBBMM occurrence distribution in her second year was just 477 m. The farthest GPS location from the Sibaya female's natal nest was 82 km, and the Euclidean distance from her natal site to the centroid of her 95% dBBMM occurrence distribution in her second year was 66 km. Finally, we could not calculate distance between the Mt. Edgecombe female's natal site and a second-year distribution centroid, but the farthest GPS location from the nest was 220 km.

We colour-ringed 76 nestling woollynecks from 38 nesting attempts at 30 nest sites. We recorded 101 colour-ring resightings and two mortalities of 38 immature woollyneck individuals between 23 December 2022 and 17 November 2024 (Figure 4.3). The two mortalities were of two juveniles found dead less than 500 m from their natal nest within one month of fledging. Both had sustained fatal leg injuries. Nearly half (48%) of resightings were <3 km of the natal nest (Figure 4.4). For the remaining 52% of resightings that were ≥3 km from the natal nest, the mean Euclidean distance from the natal site was 26.5 ± 16.9 (SD) km (*n* = 52; range: 4–98 km). The oldest resighted individual was observed 711 days after fledging. The sex ratio of individuals resighted ≥3 km from the natal site was biased toward females (64% female: 36% male). Most (91%) of resightings that were ≥3 km from the natal site were in a northeasterly direction and toward the coast.

We recorded minimum dispersal ages for four individuals, which were resighted 17–25 km from their natal nests 56–96 days after fledging. Conversely, one of the oldest resighted individuals was within 5 km of its natal site 657 days after fledging. Three individuals (including two that originated from the same nest site in different years) were subsequently observed at their natal nest with their parents during the breeding season after they fledged. One individual returned to its natal area and was observed with its parents 249 days post-fledging after having moved as far as 27 km from the nest. However, it was subsequently observed >25 km from the natal site on four occasions up to 610 days post-fledging. In four cases, siblings were observed together 180–268 days after fledging, and all were 26–30 km from their natal sites. Finally, because we relied on public reporting for resightings, we cannot be confident that group sizes were reported accurately and with every observation. Still, a minimum of 38% of resightings were of individuals in groups ranging from 6–100 storks.

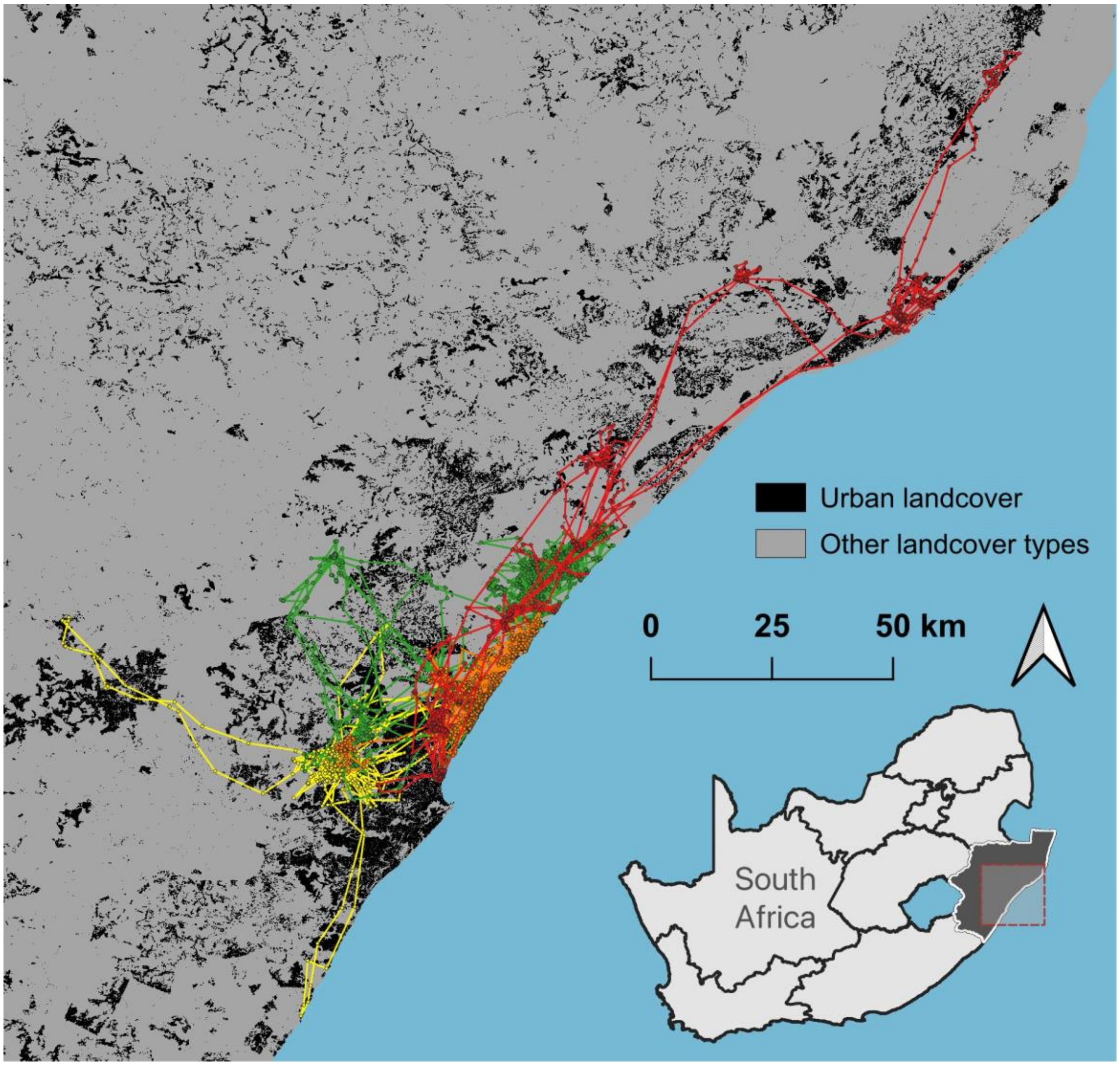

Figure 4.2: GPS locations and tracks of four immature, female African Woolly-necked Storks in KwaZulu-Natal, South Africa. (Note: Orange = Forest Hills, yellow = Kloof, red = Mt. Edgecombe, and green = Sibaya).

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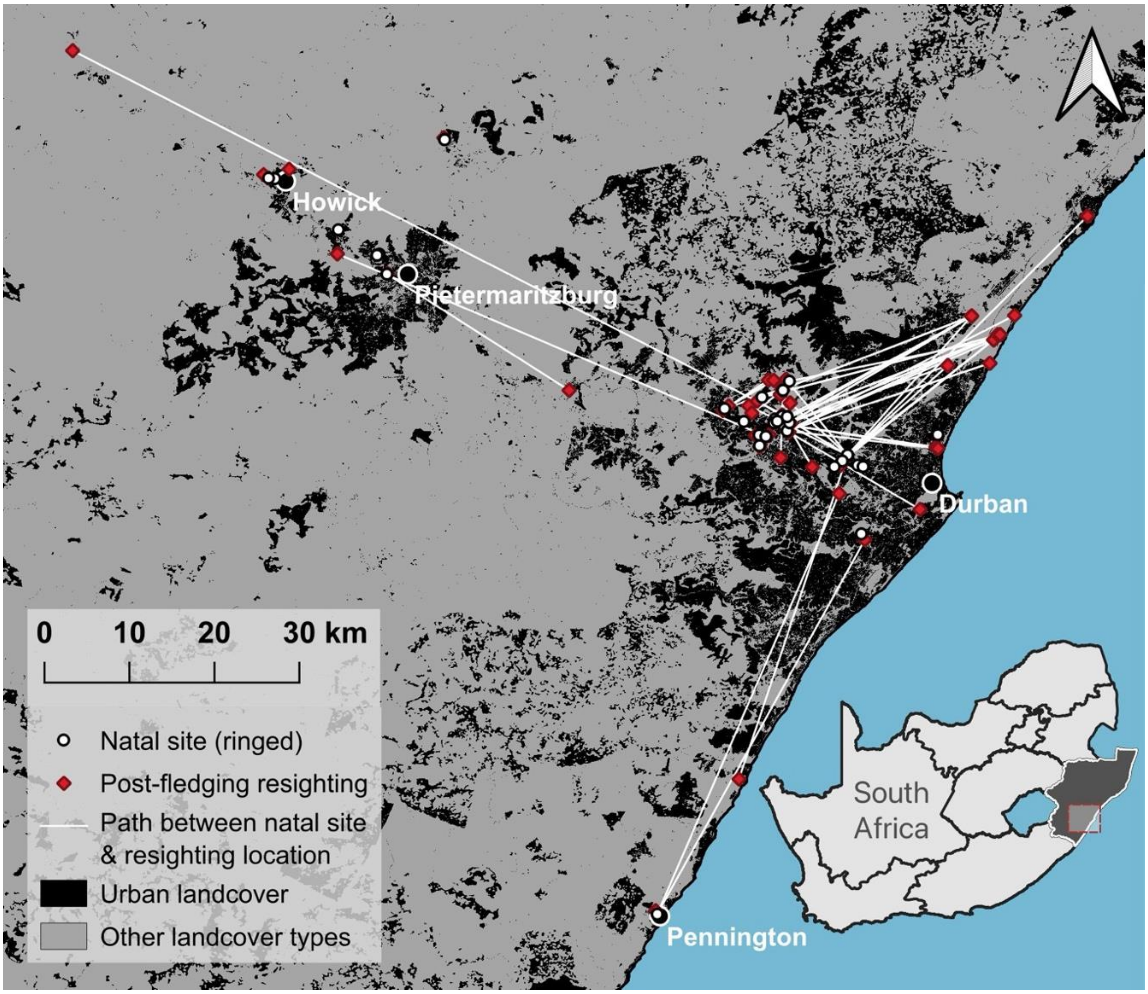

Figure 4.3: Sites of immature African Woolly-necked Stork natal sites (i.e., where colour-ringed) and subsequent resightings, with white paths connecting natal sites and resightings of individual storks.

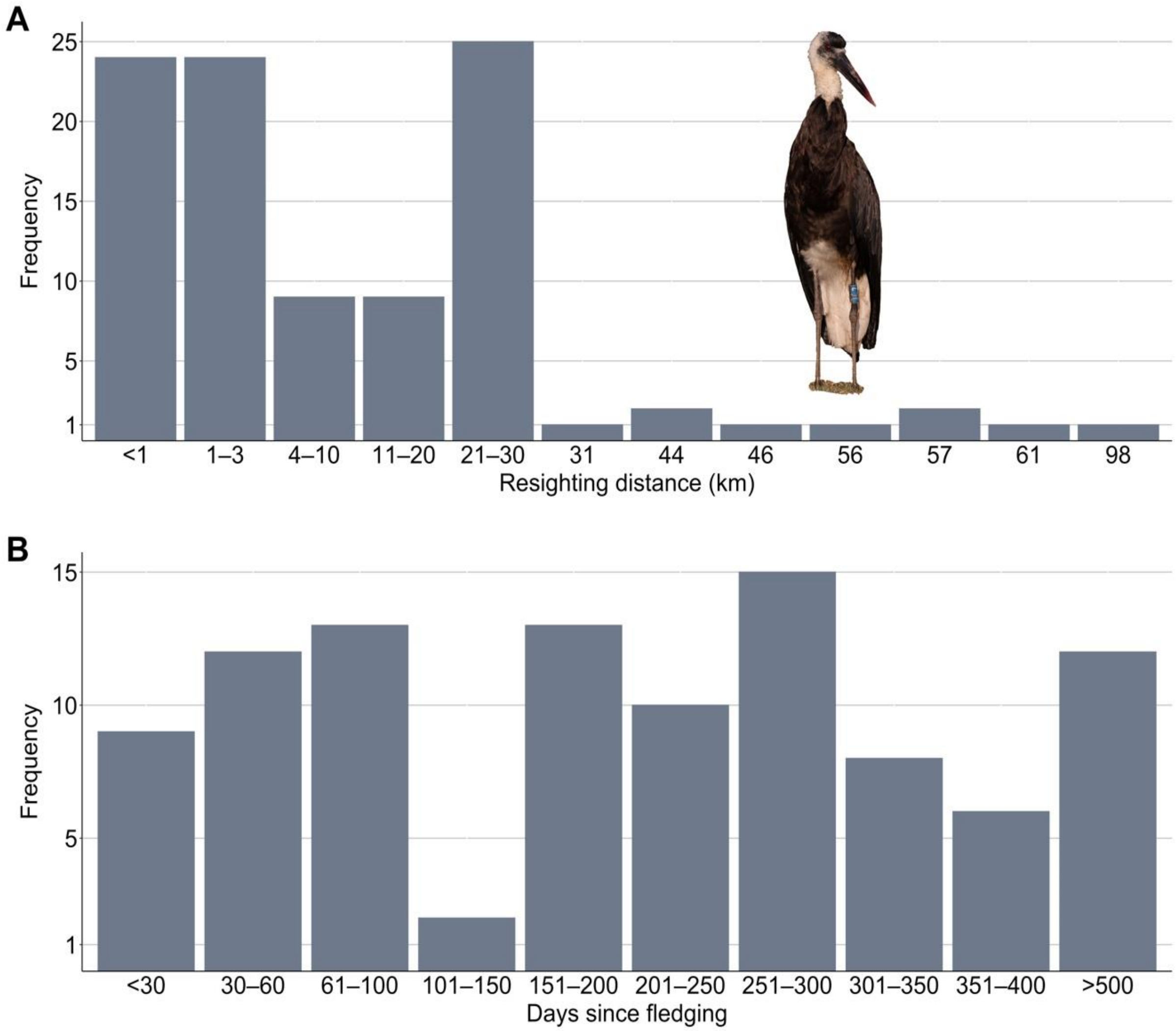

Figure 4.4: (A) Euclidean distances between natal site and resighting location and (B) timing of resighting for colour-ringed, immature African Woolly-necked Storks in KwaZulu-Natal, South Africa.

4.4.2 Nocturnal roost site fidelity

We recorded 167 nocturnal roost sites over 2,181 roost-nights from the four GPS-tracked immature woollynecks, with a mean of 545 nights per individual (range: 369–712). We recorded 39 instances in which a woollyneck was clearly disturbed from its initial roost and moved to a second site in the middle of the night. We excluded these secondary roosts from analyses because they were not initially selected as a site. The mean number of nocturnal roost sites per individual for a one-year period was 34 (range: 6–54), but for the total tracking period, the mean number of nocturnal roosts was 42 (range: 8–62). One woollyneck (Kloof) had extreme nocturnal roost fidelity, roosting at one site on 96% of nights ($n = 642$ nights). In this case, the roost site was her natal nest site, and she shared it with her parents. The other three individuals had very unstable roost site fidelity, in which 39–63% of sites were used only once. However, 3–5 roost sites were used on 52–54% of nights. Roosts were located in mixed landuse areas (32.9%), agricultural areas (22.8%), wetlands (10.2%), residential gardens (9%), coastal forests (9%), golf courses (7.8%), riparian areas (3.6%), roadside trees (3%), and urban green spaces (1.8%)

4.5 Discussion

Our study was the first to investigate the movement of immature woollynecks during their dispersial period. Immature woollynecks moved far from their natal areas, as confirmed by both high-resolution telemetry data and low-resolution colour-ring resightings, which lends support to our suggestion that dispersal contributed to the expansion of the population in KwaZulu-Natal. In combination with high breeding success in some years (Chapter 3), we have elucidated two mechanisms that certainly allowed for rapid geographic and demographic population growth. In considering the expansion in the light of invasion biology, we must recognise that dispersal rates of individuals in the invasion vanguard will be higher than those behind the invasion front (Lindström et al. 2013). Therefore, our measures of woollyneck dispersal at present–although relatively far distances compared with adult movement (Chapter 4)–are probably an underestimate of dispersal by woollynecks during the initial colonisation period 20–30 years ago.

We recognise that our measures of dispersal are not ultimate because most ringed storks were less than one-year-old by the end of our study, had not yet bred, and may not have dispersed completely yet. Given a more extended observation period for gathering resightings, our average resighting distance may increase as the younger cohort begins exploratory movements further afield. The use of mark-recapture/resight methods like colour-ringing for studying dispersal inevitably is biased toward shorter-distance-dispersers (Badia-Boher et al. 2023, Lorenz et al. 2024, Van Noordwijk 1995). This issue is exacerbated in our cases because most observers were likely in urban areas that were nearer to the natal sites. The fact that one tracked female moved as far as 220 km from the natal site demonstrates that our area of interest for soliciting colour-ring resightings should ultimately have been the whole of KwaZulu-Natal.

Exploratory movements characterise the dispersal period of many immature animals, and this results in the common finding that immatures have larger ranges than adults (compare with adult woollynecks in Chapter 5; Belthoff et al. 1993, Debeffe et al. 2013, Stewart et al. 2022). Our finding of the dispersal potential of immature woollynecks also aligns with other studies on dispersal of immature waterbirds, including other stork species (Chernetsov et al. 2006, Deguchi et al. 2022, Manikowska-Ślepowrońska et al. 2021, Väli et al. 2024). In most bird species, natal dispersal is female-biased (Clarke et al. 1997, Greenwood 1980). We had a relatively small sample size of individuals resighted ≥3 km from their natal site, but there was a bias toward females, although much more data are needed to explore the significance of this difference statistically. The lack of males in our telemetry sample was also problematic for comparative purposes. What ecological reason would account for female-biased dispersal in woollynecks is unclear because we have seen no evidence of territoriality or differences in the roles of sexes in breeding. However, there seem to be unknown social dynamics in the urban woollyneck population, as evidenced by common roost sites (also see Chapter 5), including at nests of untagged storks. The apparent tendency of immatures to gather in groups, especially at regular sites (pers. obs.) is not unexpected for young waterbirds (Gula et al. 2022), but is suggestive of an important social network. Further observations of gatherings at active nest sites with no antagonism (JG unpub. data) call into question what would drive sex-biased dispersal of woollynecks in the absence of territorial behaviour.

The briefness of our study precludes a complete understanding of the dynamics of KwaZulu-Natal's woollyneck population, especially because the species is likely long-lived, which means more time is required to understand ultimate dispersal patterns. Continuing the colour-ringing and resighting effort is essential to understand dispersal dynamics in a population that would seem to not be constrained by food resources nor territoriality. Another major missing piece of the urban woollyneck puzzle is how survival has influenced population growth. Despite the general finding that the mortality risk for young, dispersing wildlife is high (Cilimburg et al. 2002, Johnson et al. 2009, Morales-González et al. 2022, Warren and Baines 2002), we expect that for highly dispersive immature woollynecks, survival must be high to have allowed for such rapid colonisation and southward expansion. Eventually, colour-ring resights will provide sufficient data to address this yet unstudied component of the urban-colonised woollyneck population in KwaZulu-Natal.

4.6 Acknowledgements

We are grateful to the University of KwaZulu-Natal (ZA) and the National Research Foundation (ZA, Grant 9844) for funding, as well as the Ford Wildlife Foundation (ZA) for vehicle support. We thank the U.S. Fulbright programme for supporting Jonah's research. We thank Themba

Manzini for climbing to stork nests for us, to the many residents who allowed access to nests or allowed us to capture storks at their homes, and to Maryanne Anderson and Ntando Makhathini for assistance with capturing and handling storks.

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CHAPTER 5

Spatial use of adult African Woolly-necked Storks (*Ciconia microscelis*) following urban colonisation in South Africa

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Running header: Urban Woolly-necked Stork spatial ecology

5.1 Abstract

African Woolly-necked Storks (*Ciconia microscelis*) were conventionally considered shy and secretive, occurring in natural wetlands and swamp forests. However, these storks rapidly colonised urban areas of KwaZulu-Natal, South Africa, during the past three decades. We studied the post-colonisation spatial use of adult Woolly-necked Storks, hypothesising that the abundance of urban foods (e.g., supplementally-fed anthropogenic food, refuse, and natural prey in residential gardens) has led them to be highly sedentary. Using global positioning system (GPS) telemetry, we found that these storks had a mean 95% home range of 4.37 km^2, and a mean 50% core area of 33.8 ha. Only the 50% core area size significantly differed between the breeding ($\bar{x} = 99.0$ ha) and non-breeding seasons ($\bar{x} = 29.3$ ha). The mean foraging trip duration while breeding significantly differed between the incubation (2.86 h) and nestling (2.18 h) stages. Nesting storks moved an average of 0.82 km from the nest during foraging trips, and this did not significantly differ between the incubation and nestling stages. Storks used an average of 6.86 nocturnal roost sites over a year, with all individuals using just 2–3 roosts on more than 50% of nights. Although comparative data are lacking from Woolly-necked Storks in 'natural' habitats, our storks had relatively limited spatial use for their body size. The African Woolly-necked Stork is an unusual example of a large bird that has benefited from urban development, so much so that they can be highly sedentary, finding all the resources they require in small home ranges.

Keywords: Ciconiidae, home range, movement, nesting, roosting, South Africa

5.2 Introduction

Wildlife in urbanised areas face novel challenges and/or opportunities compared with their rural counterparts. The most successful species in urban environments are usually generalists and those with greater behavioural plasticity (Lowry et al. 2013, Miranda 2017, Rodewald and Gehrt 2014), likely because of the marked differences from ‘natural’ habitats, such as resource provisions (e.g., food and breeding sites), human disturbance (e.g., interactions and noise pollution), and conspecific densities, to name a few. Behavioural plasticity is an especially important characteristic that allows wildlife to successfully colonise and establish populations in urban areas where they previously did not occur (Evans et al. 2010, Mazza and Šlipogor 2024). In modifying their behavioural ecology in adjustment with the urban environment, these populations are then most likely to continue expanding, geographically and demographically (Evans et al. 2010).

One pronounced way in which some species demonstrate behavioural plasticity in urban areas is their spatial use. In many cases, urban environments have concentrated and abundant food (natural and/or anthropogenic) and breeding sites (natural and/or artificial), which theoretically requires less movement to locate these resources. As a consequence, many urban wildlife populations have reduced spatial use compared with rural populations (Mannan and Boal 2000, Šálek et al. 2015, Streicher et al. 2021). Even when a species may not necessarily benefit from concentrated resources in urban areas, mosaic landscapes that feature urban habitat interspersed with green spaces can provide sufficient habitat heterogeneity so that predators such as raptors do not have to move across large home ranges (McPherson et al. 2019, Roth et al. 2008).

Despite rapid urban land expansion in Africa (Gao and O’Neill 2020), there is growing evidence of large avian species persisting in, adapting to, and colonising African urban areas (Downs et al. 2021, Henriques et al. 2018, Holbech and Cobbinah 2021, Pomeroy and Kibuule

2017, Suri et al. 2017). African Woolly-necked Storks (*Ciconia microscelis*; hereafter, 'woollyneck') were conventionally described as shy and secretive, especially during nesting (Brown et al. 1982, Hancock et al. 1992, Scott 1975). However, in the past few decades the species rapidly colonised KwaZulu-Natal Province in South Africa, particularly urban areas, where they have taken to supplemental feeding by humans (Thabethe and Downs 2018). Besides widely available food, which also includes common garden animals such as frogs, lizards, and moles and refuse at landfills and compost dumps (pers. observ.), the establishment of abundant nesting sites (i.e., large, non-native trees in gardens) has likely created novel habitat for woollynecks in the region (Chapter 3).

The rapid adjustment of woollynecks to urban KwaZulu-Natal has led to population expansion across a human-altered landscape mosaic unlike anywhere else described in Africa. We sought to understand how the apparent saturation of food and nesting sites for woollynecks across this landscape has affected their spatial use following the establishment of an urban population. Following the aforementioned findings of much reduced spatial use in other urban wildlife globally and in KwaZulu-Natal, we used global positioning system (GPS) telemetry to test the hypothesis that adult woollynecks have become highly sedentary because of abundant urban resources. Besides small home ranges, we expected breeding woollynecks to have short foraging trips in close proximity to their nests, especially while provisioning nestlings with anthropogenic food and natural prey found in residential gardens. Further, we studied roost site fidelity as another measure of sedentary behaviour in urban areas. While this study contributes to the growing understanding of urban waterbirds in the tropics, it is also the first of its kind for woollynecks in Africa and provides a first-look into previously undescribed aspects of the species' ecology.

5.3 Methods

5.3.1 Study area

We studied the movement of woollynecks captured in the municipalities of eThekwini and Richmond, KwaZulu-Natal Province, South Africa (Figure 5.1). This region is characterised by a subtropical climate. Mean annual rainfall in the city of Durban (eThewkini Municipality) is 893 mm, and mean annual minimum and maximum temperatures are 13.7° C (July) and 27° C (February), respectively (https://en.climate-data.org/africa/south-africa/kwazulu-natal/durban-511/). The eThewkini Municipality is a mosaic of mixed urban and suburban land use whereas the Richmond Municipality is characterised by rural residential areas and agriculture. Population density across the study area in 2022 varied from 50 people/km^2 in the Richmond Municipality to 1,851 people/km^2 in the eThekwini Municipality (Statistics South Africa 2023).

5.3.2 Movement data collection

Between August 2022 and October 2023, we captured adult woollynecks in residential gardens using a net walk-in trap or a custom foot-noose trap made of a garden trellis and monofilament line. We attracted woollynecks to the traps using bait for both techniques. Once captured, we fitted woollynecks with one of two models of GPS/GSM telemetry transmitters (Sigfox 0G Technology, Randburg, South Africa, 85 g, or Druid Technology, Shenzhen, China, 28 g), which we attached using a Teflon® or Spectra® harness in a backpack-chest-harness style (Mielke and Handschuh 2018). We programmed transmitters to record a location every 30 min during day and night. We aged individuals as adults by their white foreheads and red eyes, whereas juveniles (less than one year old) have a black forehead continuous with the black cap and have brownish eyes. Shortly before one year of age, the forehead becomes streaked with white as it transitions to adult colouration (pers. obs.) We collected a blood sample on FTA® paper from the brachial vein of each captured woollyneck, and subsequently extracted DNA using an E.Z.N.A.® extraction kit (Omega Bio-tek, Inc., Georgia, USA), following the manufacturer's protocols. We sent samples to a commercial lab for molecular sexing (Molecular Diagnostics Services Pty Ltd, Westville, South Africa). We also fitted each captured woollyneck with a unique alpha-numeric colour ring and measured body mass before releasing within 20 min of capture.

5.3.3 Home range estimates

After filtering erroneous GPS locations, we limited all home range analyses to diurnal GPS locations by filtering data to the period from 30 min before sunrise to 30 min after sunrise on the online platform *MoveApps* (Kölzsch et al. 2024) using the "Upload File from Local System" and "Filter/Annotate Day or Night" apps (Kölzsch 2024, Kölzsch and Scharf 2023). We estimated individual annual home ranges of woollynecks using the R package *ctmm* (Calabrese et al. 2016) in R version 4.3.1 (R Core Team 2023). First, we calculated variograms of each individual's movements to determine range residency. We subsequently fit continuous movement models for all adults because they were range residents. We estimated 95% and 50% home ranges using autocorrelated kernel density estimation (AKDE; Fleming et al. 2015) using the perturbative Hybrid Residual Maximum Likelihood (pHREML) parameter estimator because it reduces biases in home range estimation compared with other maximum likelihood estimators (Silva et al. 2022). We chose the AKDE method because it accounts for spatial and temporal autocorrelation, which was prevalent because of our high frequency of GPS fixes.

In addition to estimating total home range sizes, we binned GPS locations from the first year of tracking adults into two seasons, breeding (August–January) and non-breeding (February–July), and followed the same workflow to estimate seasonal home ranges using

AKDE. Because *t*-test assumptions were violated, we used a randomisation test (Manly 1997) to test if there was a difference in home range sizes between the breeding and non-breeding seasons, using the difference between the means of each season as the test statistic. Because of our small sample size and uneven sex ratio of tracked woollynecks, we did not test the influence of sex on home range sizes. For all means, we bootstrapped 95% confidence intervals (CI).

5.3.4 Nesting foraging trips

We used the R package *track2KBA* (Beal et al. 2021) to summarise foraging trips away from nests by woollynecks. Firstly, we filtered telemetry data for each nesting woollyneck to the known time periods of two nesting stages (incubation and nestling) based on detailed field monitoring of nests (Chapter 3). One individual laid eggs that never hatched, but they continued to incubate beyond 30 days. For this case, we limited analyses to the 30 days after incubation began to reflect the usual period. We binned telemetry data for each nesting stage separately to test if time away from the nest varied between these periods. Within *track2KBA*, we specified locations outside a 100 m buffer around the nest to count as a trip so as to account for GPS error and perching in the vicinity of the nest. We specified 1 h as a minimum trip duration to account for the temporal resolution of the telemetry data (i.e., locations every 30 min). Outputs estimated with *track2KBA* included the number of unique trips, duration, and maximum Euclidean distance travelled from the nest on each trip. Because some transmitters failed to acquire GPS locations sometimes, especially in the canopy of a nest tree, we manually assessed the trip summary outputs from *track2KBA* and compared them with the raw telemetry data to remove trips that were erroneously classified as trips because of gaps in GPS locations. We summarised means of trip metrics as well as looked at trends in trips over the nesting period. We did not estimate a mean number of trips per day for the Sigfox transmitters because of gaps in the data in which trips were likely not recorded. We used a randomisation test (Manly 1997) to compare trip duration and maximum distance between the incubation and nestling periods, using the difference between the means of each stage as the test statistic. For all means, we bootstrapped 95% confidence intervals (CI).

5.3.5 Nocturnal roost site fidelity

To determine nocturnal roost site locations of woollynecks, we filtered telemetry data to the period from 30 min after sunset to 30 min before sunrise on the online platform *MoveApps* (Kölzsch et al. 2024) using the “Upload File from Local System” and “Filter/Annotate Day or Night” apps (Kölzsch 2024, Kölzsch and Scharf 2023). We limited analyses of nocturnal roost sites to a one-year period after capture. We excluded solitary GPS locations from nocturnal roost transition movements because they represented instances when woollynecks were disturbed from their roost and moved in the middle of the night (see Results). We created centroids of nocturnal GPS location clusters to identify distinct roost sites for each individual woollyneck. We defined a roost site as anything within a 30 m buffer of the centroids, and calculated the number of unique nights that each stork spent at a given roost site. We classified roost sites into habitat categories and estimated roost site fidelity as the number of nights used divided by the total number of nights an individual was recorded roosting. We performed all analyses of nocturnal roosts in QGIS 3.18 (QGIS Development Team 2021).

5.4 Results

We used 80,447 diurnal (range: 3,706–17,381 per individual) and 39,829 nocturnal (range: 2,274–7,982 per individual) GPS locations from seven adult woollynecks (five females, two males; Figure 5.1) in our analyses. The SigFox transmitters frequently failed to record GPS locations, especially later in their deployment, hence the variation in the number of locations per individual. The mean tracking time was 560 days (range: 289–750). Two females died of unknown causes after 569 and 592 days of tracking, and one male's transmitter failed after 289 days.

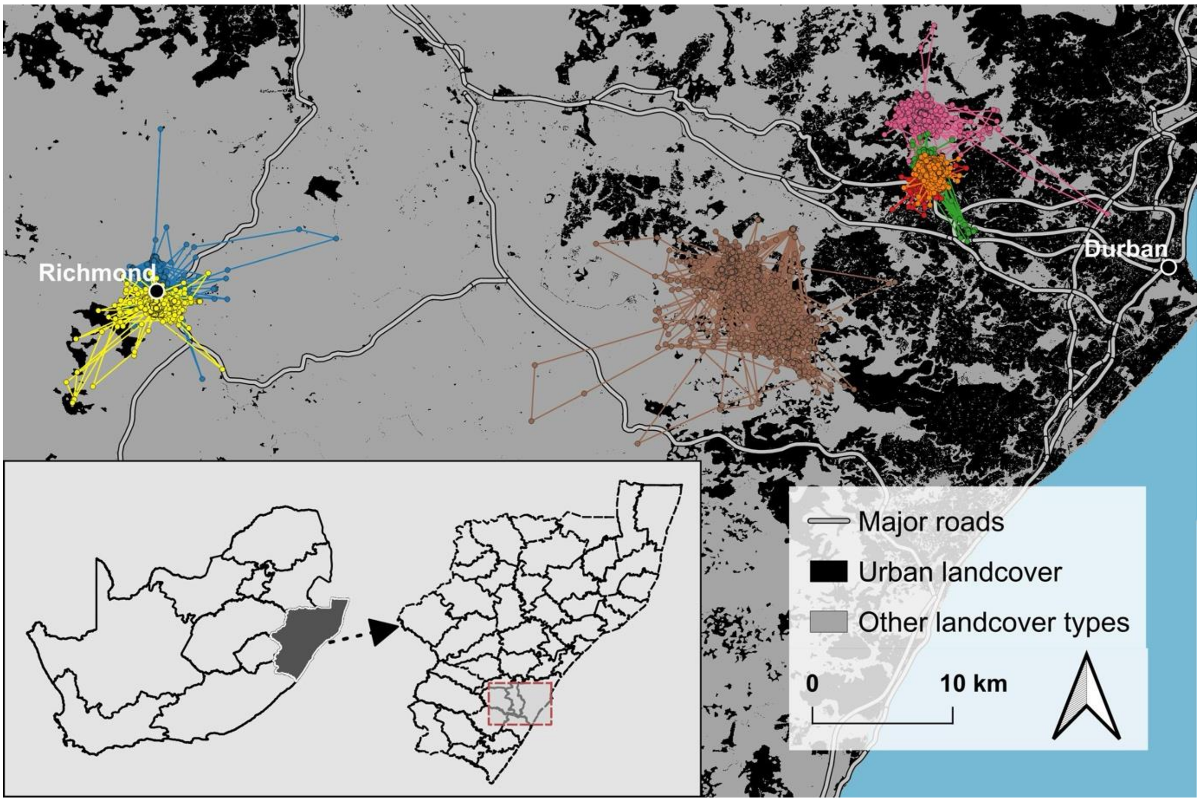

Figure 5.1: GPS locations and tracks of seven African Woolly-necked Storks (each colour represents an individual) in KwaZulu-Natal, South Africa.

5.4.1 Home range estimates

The mean 95% home range for adult woollynecks was 4.37 km^2 (95% CI: 0.96–9.73 km^2), and the mean 50% core area was 33.8 ha (95% CI: 12.5–56.9 ha). The 95% home range size mean was skewed by a peri-urban female (Shongweni) with a home range of 19.68 km^2, magnitudes larger than the more urban storks (Table 5.1). The median 95% home range size was 1.10 km^2, and the median 50% home range size was 13.5 ha. There was no difference (test statistic = -6.30, $p = 0.42$) between 95% home ranges during the breeding ($\bar{x} = 7.94$ km^2, 95% CI: 1.18–20.21 km^2) and non-breeding seasons ($\bar{x} = 1.64$ km^2, 95% CI: 0.12–3.50 km^2)

over a one-year period. However, the 50% core home range during the breeding season ($\bar{x}$ = 99.0 ha, 95% CI: 51.7–144.6 ha) was significantly larger (test statistic = -69.7, *p* = 0.046) than during the non-breeding season ($\bar{x}$ = 29.3 ha, 95% CI: 11.6–52.3 ha) over a one-year period (Supplementary information Table S5.1).

Table 5.1: Body mass, tracking duration, and home range sizes of seven adult African Woolly-necked Storks in KwaZulu-Natal, South Africa, derived from autocorrelated kernel density estimation. Estimates are in bold and reported with lower and upper confidence intervals.

Individual (Sex)	Body mass (g)	Tracking duration (days)	95% home range (km^2)	50% home range (ha)
Bromhead (Male)	2,240	750	**0.87** (0.86, 0.89)	**10.2** (10.1, 10.3)
Fairview (Female)	2,270	365	**0.99** (0.95, 1.03)	**10.6** (10.5, 10.7)
Buckingham (Female)	2,140	729	**0.72** (0.69, 0.76)	**9.1** (9.0, 9.3)
Waterfall (Female)†	1,970	569	**1.10** (1.07, 1.13)	**13.5** (13.3, 13.6)
Richmond (Female)†	1,960	592	**1.36** (1.32, 1.39)	**23.7** (23.5, 23.9)
Richmond (Male)	-	289	**5.87** (5.58, 6.18)	**89.0** (87.0, 90.0)
Shongweni (Female)	1,580	623	**19.68** (18.93, 20.44)	**81.0** (80.0, 82.0)

†died

5.4.2 Nesting foraging trips

We recorded foraging trips of six nesting woollynecks (five females, one male) during eight nesting attempts (three in 2022, five in 2023; Table S5.2). These data included six incubation stages and six nestling stages. Trip duration ranged from 1–27 h, and the maximum distance travelled from the nest ranged from 103 m to 15.7 km. The longest and farthest trips were predominantly undertaken by a female (Shongweni) in a peri-urban area. As confirmed by field observations, she and her mate alternated full days of nest attendance while the other foraged elsewhere, predominantly at a house where they were supplementally fed. When not at the nest, she roosted overnight far from the nest before returning to take over incubation duty from her mate in the morning. Foraging trip duration during the incubation stage ($\bar{x} = 2.86$ h, 95% CI: 2.45–3.35, $n = 302$) was significantly greater (test statistic = -0.68, $p < 0.001$) than during the nestling stage ($\bar{x} = 2.18$ h, 95% CI: 2.03–2.33, $n = 674$). The maximum distances of foraging trips were not significantly different (test statistic = -0.06, $p = 0.51$) between the incubation ($\bar{x} = 0.86$ km, 95% CI: 0.71–1.03, $n = 302$) and nestling stages ($\bar{x} = 0.80$ km, 95% CI: 0.73–0.89, $n = 674$). Therefore, the overall mean maximum distance per trip was 0.82 km. For the three females with Druid transmitters, the mean number of foraging trips per day was 1.77 during the incubation stage and 1.93 during the nestling stage.

5.4.3 Nocturnal roost site fidelity

We recorded 48 nocturnal roost sites during 2,026 stork-nights from seven adult woollynecks, with a mean of 289 nights per individual (range: 147–366). Two roosts were used by up to three individuals on different nights, and two storks roosted together on several nights at each of those roosts. We recorded 13 instances in which a woollyneck was disturbed from its initial roost and moved to a second site in the middle of the night. We excluded these secondary roosts from analyses because they were not selected as a site initially. The mean number of nocturnal roost sites per individual throughout a year per was 6.86 (range: 4–13), but this was skewed by the one peri-urban female (Shongweni) that had 13 nocturnal roosts whereas the more urban storks only had 4–7 roosts. All woollynecks had 2–3 roosts that they used on more than 50% of nights. The habitat categories where roosts were located included residential gardens (47.9%), riparian zones (20.8%), mixed land use woodlands (10.4%), cliff/canyon forests (8.3%), roadside trees (6.3%), golf courses (4.2%), and schools (2.1%).

5.5 Discussion

The urban colonisation by woollynecks in KwaZulu-Natal, South Africa, is unprecedented in Africa as far as we know. Not only was ours the first study on the spatial use of woollynecks in an urban environment, but it was also the first time movements of woollynecks have been investigated in Africa. We found that urban woollynecks had relatively small home ranges, high nocturnal roost fidelity to just a few sites, and restricted movements during nesting. Apparently, urban KwaZulu-Natal is resource-dense for woollynecks, allowing them to have a sedentary lifestyle, which is in line with our hypothesis. The profusion of resources in urban areas (Thabethe and Downs 2018), lack of territorial behaviour (pers. obs.), and small home ranges have allowed for the establishment of a high density of woollynecks in urban KwaZulu-Natal, which matches a common pattern of urbanised bird populations globally, including other stork species (Evans et al. 2010, López-García and Aguirre 2023, McPherson et al. 2019, Møller et al. 2012, Pomeroy and Kibuule 2017, Stout and Rosenfield 2010).

Globally, there are at least four other stork species–White Storks (*C. ciconia*), Marabou Storks (*Leptoptilos crumenifer*), Greater Adjutants (*L. dubius*), and Wood Storks (*Mycteria americana*)–that use urban areas and have experienced positive effects on some populations (Evans and Gawlik 2020, López-García and Aguirre 2023, Pomeroy and Kibuule

2017, Singha et al. 2003). Like these species, one significant contributor to the success of woollynecks in urban KwaZulu-Natal is artificial food sources. However, unlike other species, woollynecks are the only storks known to benefit from widespread supplemental feeding by human residents (Thabethe and Downs 2018). While a phenomenon akin to a 'luxury effect' (Hope et al. 2003) probably plays a role to a certain extent, in which supplemental feeding and therefore woollyneck densities are more prominent in wealthier neighbourhoods, the urban matrix is also profuse with natural prey items (e.g., frogs, reptiles, insects, and rodents), which are particularly important for woollynecks provisioning nestlings (Thabethe et al. 2021). So although year-round, daily feeding (Thabethe and Downs 2018) certainly influences the restricted spatial use of woollynecks, an abundance of natural food also serves to enhance the quality of urban habitat.

The lack of comparative spatial use data from woollynecks in non-urban Africa, such as natural wetland systems where they historically occurred, is a weakness of our study. Asian Woolly-necked Storks (*C. episcopus*) in natural areas of Cambodia had much larger home ranges than we found for the African species in urban areas, and White Storks using anthropogenic food sites travelled relatively far distances from their nests (Gilbert et al. 2016). Although we tracked one peri-urban female woollyneck, we did not have a sufficient sample of individuals to compare the spatial use of woollynecks in urbanised, residential areas. Capturing rural woollynecks proved difficult because they were wary and not used to being fed, whereas urban woollynecks readily came to food used as bait at traps. Unfortunately, we could not overcome this bias. We find it unlikely that movements of woollynecks in natural habitats could be as limited as urban individuals because the small home range sizes we found are the most restricted movements described for any stork species (see Supplementary data in Gula et al. 2023). Nonetheless, there will be value in studying movement in a 'natural' area's population.

Understanding how differences in the environment influence spatial use during the nesting period will be particularly useful, as many studies of wildlife across urban gradients have found important differences in ecology (Clément et al. 2021, Šálek et al. 2015; cf. Zurell et al. 2018). For example, the prolonged foraging trips that we found for the peri-urban female during nesting may be representative of ‘natural’ populations, as there is some evidence of this type of behaviour in at least two other African stork species (Gula et al. 2024; unpub. data). In contrast, the short, frequent trips made by urban woollynecks reflect the abundance and distribution of food around urban nesting sites. Additionally, comparing nocturnal roosting behaviour across a landscape gradient will also shed light on population differences. The ‘communal’ roost sites we found in common for our tracked woollynecks are not unusual for the species in our study area (pers. obs.). Whereas the high density of woollynecks in urban KwaZulu-Natal may result in an important social network stemming from communal roosts and foraging sites, the overall low densities found in ‘natural’ habitats (Hancock et al. 1992) may mean entirely different social dynamics that are worth investigating.

Based on conventional descriptions of woollynecks (Brown et al. 1982, Hancock et al. 1992, Scott 1975), their success in urban KwaZulu-Natal is surprising and contrary to how the species was historically perceived. Yet this success demonstrates that the conservation community should not necessarily assume that urbanisation will negatively impact all wildlife species, including if a species has never encountered urbanisation before. Assuming the behavioural plasticity of KwaZulu-Natal’s woollynecks is not linked to genetics within the South African population (Lowry et al. 2013, Møller 2008, Partecke et al. 2006), woollyneck urbanisation in KwaZulu-Natal potentially has positive implications for populations elsewhere in Africa. Whether further urban expansion occurs in South Africa–as with other urban pioneering species in the country (Duckworth et al. 2010)–or populations elsewhere in sub-Saharan Africa follow similar assimilation into growing urban areas, more research will only serve to enhance our understanding of this understudied species in both historical and novel environments as well as how different populations will respond to habitat changes.

5.6 Acknowledgements

We thank the University of KwaZulu-Natal (ZA) and the National Research Foundation (ZA, Grant 9844) for funding, as well as the Ford Wildlife Foundation (ZA) for vehicle support. We thank the U.S. Fulbright programme for supporting Jonah's research. Thanks to Themba Manzini for climbing to stork nests for us, to the many residents who allowed access to nests or allowed us to capture storks at their homes, and to Maryanne Anderson and Ntando Makhathini for assistance with capturing and handling storks.

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5.8 Supplementary information

Supplementary information Table S5.1. Seasonal home range size estimates of African Woolly-necked Storks in KwaZulu-Natal, South Africa.

Individual (Sex)	**Breeding AKDE 95% home range (km^2), (LCI, UCI)**	**Breeding AKDE 50% home range (km^2), (LCI, UCI)**	**Non-breeding AKDE 95% home range (km^2), (LCI, UCI)**	**Non-breeding AKDE 50% home range (km^2), (LCI, UCI)**
Richmond (Female)	1.67 (1.60, 1.74)	0.253 (0.25, 0.257)	1.43 (1.36, 1.50)	0.206 (0.203, 0.210)
Buckingham (Female)	0.88 (0.83, 0.94)	0.111 (0.108, 0.113)	1.88 (1.65, 2.13)	0.37 (0.35, 0.39)
Fairview (Female)	1.28 (1.22, 1.34)	0.146 (0.144, 0.148)	0.48 (0.44, 0.52)	0.056 (0.054, 0.057)
Bromhead (Male)	0.96 (0.92, 1.00)	0.088 (0.087, 0.090)	0.65 (0.62, 0.68)	0.079 (0.078, 0.081)
Shongweni (Female)	44.17 (41.52, 46.90)	4.15 (4.07, 4.24)	0.051 (0.048, 0.054)	0.030 (0.030, 0.031)
Waterfall (Female)	1.60 (1.54, 1.67)	0.111 (0.110, 0.113)	1.80 (1.66, 1.95)	0.35 (0.34, 0.36)
Richmond (Male)	5.03 (4.71, 5.35)	0.64 (0.63, 0.66)	6.61 (6.10, 7.14)	0.95 (0.92, 0.97)

Supplementary informationTable S5.2. Summaries of foraging trips during nesting by African Woolly-necked Storks in KwaZulu-Natal, South Africa.

Individual (Sex) and nesting year	**Nesting stage**	**No. trips recorded**	**Mean trip duration ± SD (h)**	**Mean maximum trip distance ± SD (km)**	**Maximum trip distance (km)**
Fairview (Female) 2022	nestling	110	2.27 ± 1.65	0.79 ± 0.53	3.53
Bromhead (Male) 2022	incubation	48	1.79 ± 0.81	0.50 ± 0.27	1.34
Bromhead (Male) 2023	incubation	69	1.78 ± 0.88	0.59 ± 0.37	2.13
Bromhead (Male) 2023	nestling	263	2.09 ± 1.48	0.62 ± 0.41	3.17
Buckingham (Female)2022	incubation	30	2.20 ± 1.41	0.57 ± 0.33	1.32
Buckingham (Female)2022	nestling[†]	13	3.00 ± 2.20	0.60 ± 0.26	0.84
Buckingham (Female)2023	incubation	23	2.00 ± 2.26	0.42 ± 0.37	1.89
Buckingham (Female)2023	nestling	76	1.64 ± 0.84	0.51 ± 0.24	1.00
Richmond (Female)2023	incubation	53	2.59 ± 1.37	0.59 ± 0.20	0.88
Shongweni (Female) 2023	incubation	19	15.87 ± 9.14	5.6 ± 2.63	8.13
Shongweni (Female) 2023	nestling	10	10.00 ± 7.80	5.75 ± 2.65	8.35
Waterfall (Female) 2023	incubation	60	1.73 ± 1.01	0.50 ± 0.37	1.79
Waterfall (Female) 2023	nestling	175	1.84 ± 1.10	0.90 ± 1.40	15.70

CHAPTER 6

General discussion, conclusions and recommendations

6.1 General discussion

The African Woolly-necked Stork (*Ciconia microscelis*; hereafter, 'woollyneck') was historically considered to be shy and easily disturbed, especially while nesting (Brown et al. 1982, Hancock et al. 1992, Scott 1975). Ironically, the expansion of woollynecks in KwaZulu-Natal, South Africa (Thabethe 2018), from an estimated 30 breeding pairs in the 1980s (Brooke 1984) to an abundant urban bird demonstrated that the species had a much greater degree of ecological and behavioural plasticity than suspected. The success of woollynecks in urban KwaZulu-Natal follows the findings of multiple other large waterbird species that have persisted in or colonised human-dominated landscapes, in much contrast to conventional ideas of their biologies (Kittur and Sundar 2021, Koju et al. 2019, Marcelino et al. 2023, Mehta et al. 2024, Pomeroy and Kibuule 2017, Shlepr et al. 2023, Singh and Downs 2016a).

High breeding rates and natal dispersal are two main drivers of population expansion into novel habitats, especially urbanised landscapes (Evans et al. 2010). The objectives of this study were to understand how the dynamics of KwaZulu-Natal's woollyneck population could have led to the unprecedented population expansion in recent decades. The findings showed that urban woollynecks can have high fecundity in some years, which should result in high recruitment at the periphery of the species' range.

There are no apparent ecological tradeoffs of urban breeding for woollynecks, as has been found for other urban wildlife in urbanised KwaZulu-Natal (Muller et al. 2020, Pillay and Downs 2024). For the congeneric White Stork (*C. ciconia*), which has come to heavily use anthropogenic refuse sites in Portugal and Spain, the tradeoff of a diet of anthropogenic food is high breeding success at the expense of juvenile survival (López-García et al. 2021). Juvenile survival is an important missing component of woollyneck population dynamics in this study. However, the rapid population growth of woollynecks would seem to suggest high survival (Chapter 3). The apparent contrast with the situation with urban White Storks may be because, in KwaZulu-Natal, the dominance of natural prey items in the diet of nestling woollynecks (Thabethe et al. 2021) and, when provisioned, anthropogenic food that is high in fat and protein (Thabethe and Downs 2018) does not negatively impact health, as far as is known.

Immature woollynecks in this study dispersed relatively far from their natal sites in contrast with the highly sedentary movements of adults (Chapter 4 and Chapter 5). Greater movement by immature animals is not unexpected, as they usually have larger home ranges than adults in most species (Belthoff et al. 1993, Debeffe et al. 2013, Stewart et al. 2022). The behavioural plasticity of woollynecks in the urbanised population has allowed them to take advantage of resource-rich areas, such as residential gardens and urban greenspaces, where natural prey such as reptiles and amphibians are abundant and where supplemental food from humans is routine (Thabethe and Downs 2018). The apparent ease with which woollynecks may become habituated is a noteworthy behavioural change that must have worked in tandem with high dispersal to facilitate rapid population expansion (Duckworth and Badyaev 2007).

Although woollynecks in KwaZulu-Natal's mosaic landscape have already reached Evans et al.'s (2010) third phase ('spread') of urban colonisation, their future trajectory is unknown considering Downs et al.'s (2021) modification of this stage, in which urbanised populations either continue to increase, plateau, or decline over time. The generalist ecology of woollynecks makes them most likely to continue to increase or, if density-dependent mechanisms manifest, plateau. However, the population trajectory depends on a number of factors. Firstly, public perception must remain positive as they have been during the colonisation period (Thabethe and Downs 2018). Secondly, presumably, there is a limit to the level and type of urbanisation that woollynecks can tolerate. For example, nests in this study were never located in heavily urbanised and industrial areas, likely because suitable nest trees are felled in such areas. Additionally, tracked woollynecks never visited these areas but only flew over them. Finally and similarly, habitat in the mosaic landscape must remain heterogenous enough to provide suitable nest sites and provide natural foraging areas where adults can obtain prey for provisioning nestlings.

Urban ecology research generally has had a focus on human-wildlife conflict despite the need to understand how wildlife populations respond to habitat changes such as urbanisation (Perry et al. 2020). In our study area in KwaZulu-Natal especially, research has found that a diversity of taxa, including mammals (Ehlers Smith et al. 2018, Patterson et al. 2019, Rollinson et al. 2013, Streicher et al. 2021), birds (Chibesa et al. 2017, Josiah and Downs 2023, Muller et al. 2020, Singh and Downs 2016b), and reptiles (Singh et al. 2021) have persisted and thrived in the face of urbanisation. Although woollynecks have been established in KwaZulu-Natal's mosaic landscape for some time (Thabethe 2018), this study importantly shed light on their population dynamics in a landscape unlike where they occur elsewhere on the continent. Continuing to understand how they respond to further changes in this landscape will be important for woollyneck conservation in South Africa.

6.2 Conclusions

The case of the urbanised woollyneck population in KwaZulu-Natal shows that the conservation community must be cautious in its assumptions about the ecological plasticity of wildlife. Yes, woollynecks historically and presently in most of Africa avoid areas of human development and inhabit natural wetlands, but this does not preclude them from adapting to human-modified landscapes in the future. The unprecedented urban expansion of woollynecks in South Africa provides hope that such adaptation is possible elsewhere in the species' range where natural habitat may be lost or modified. In KwaZulu-Natal, the available evidence suggests that woollynecks have only benefited from urbanisation, which is an emerging finding for some other species in the country, too (Downs et al. 2021, Duckworth and Altwegg 2014, Streicher et al. 2021). This finding is supported by the potential for high reproductive output and the ability of adults to occupy small home ranges (Chapter 3 and Chapter 5).

The combination of high breeding output in some years and distant natal dispersal help explain the rapid population expansion–geographically and demographically–of woollynecks in KwaZulu-Natal. Besides the anomaly of woollynecks becoming urbanised, their expansion at the range edge contributes to the understanding of what influences range dynamics at the periphery. In this case, what was most certainly selection pressures and environmental limits to the range historically (Gaston 2003, Van Petegem et al. 2016) seem to have been overcome because of favourable habitat modification leading to behavioural changes. What remains to be seen is if this expansion will continue or if some environmental or demographic factors may ultimately be limiting.

6.3 Recommendations

Because woollynecks are permanent urban residents now, continuing to educate the public about them remains an important task. Although most people feed woollynecks acceptable food such as raw meats, some still provide bread, highly processed meats, cheese, and other items that do not contribute much nutrition to the birds. If the negative effects of supplemental feeding are to remain low, the public must be made aware of what foods are appropriate if they choose to feed woollynecks. Additionally, helping residents understand the level of habituation woollynecks can reach is key. Woollynecks can become so habituated that they enter homes and become nuisances. While this behavioural change is fascinating, it does create conflict with people in some cases. Furthermore, woollynecks nesting over driveways and homes can become a nuisance when they defecate on cars and other objects below. In some cases, this can lead homeowners to cut down nest trees. Fortunately, a KwaZulu-Natal provincial ordinance outlaws disturbing active nests in such ways, but this is not widely known. If trees must be felled, it should be done outside the nesting season. During this study, this happened to multiple nest sites, and nesting pairs simply found other nearby trees. Such tree felling is unlikely to have a major impact on the population thanks to the abundance of suitable nest trees in the study area. As long as this type of habitat modification happens at a low level, the breeding population of woollynecks will not be negatively impacted.

Although woollynecks have greatly benefited from urbanisation, there still may be tradeoffs to the urban lifestyle. For example, many storks sustain injuries that are ultimately human-caused (JG, unpublished data). Entanglement in fishing line is relatively common and leads to leg deformities and loss of feet/legs on occasion (JG, pers. obs.). Further, woollynecks sometimes are hit by cars or attacked by dogs (JG, pers. obs.), which is certainly a result of habituation to people and their vehicles and pets. In 2023, injuries of ringed and unringed woollynecks reported to JG peaked following the breeding season (unpublished data), presumably because newly-fledged juveniles are naive. These risks of an urban life demonstrate that an important next step in understanding population dynamics is to investigate immature survival. The continued colour-ringing and resighting effort will fill this critical knowledge gap and continue to shed light on the unprecedented colonisation of urban KwaZulu-Natal.

On a global scale, our literature review of stork research demonstrated most species have not been well-studied (Chapter 2). For many species, basic aspects of natural history and ecology remain unstudied, which was the case for the African woollyneck before this study. However, for the African woollyneck, there is still a need for a comparative study in natural habitats to better understand how urbanisation has changed their population ecology. Similarly, other species of storks around the world have exploited human-modified landscapes, yet research on them has been limited to a few species and mostly in the United States of America (e.g., Shlepr et al. 2023), Europe (e.g., Gilbert et al. 2016, López-Calderón et al. 2023), and south Asia (e.g., Katuwal et al. 2022, Kittur and Sundar 2020, 2021). Field studies on long-lived species like storks are labour-intensive and costly, but undertaking novel research like this study provides critical insights into how waterbirds like storks can adapt to a changing world and significantly contribute to their conservation.

6.4 References

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