Improving monitoring methods and determining the breeding success of Grey Crowned Cranes (*Balearica regulorum*) within a key agricultural area in South Africa

by

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Abstract

Endangered Grey Crowned Cranes (*Balearica regulorum*) primarily inhabit unprotected areas subject to substantial land-use transformation. With a limited understanding of this species' reproductive success, this study aimed to i) improve monitoring methods of nesting and social groupings and ii) identify this species' reproductive output in response to environmental conditions. To produce monitoring guidelines, I compared behavioural responses of pairs, families and flocks to traditional on-foot and drone monitoring. Flocks took flight at greater distances when approached on-foot than by drones, while nesting birds were more sensitive to vertical drone approach angles. Breeding metrics from 95 nest sites revealed a low overall breeding success, with most nest sites failing to transition from eggs to hatchlings. Higher success rates were found at nests closer to natural grasslands and human development. Altogether, this crane species would benefit from consistent monitoring, collaborative efforts, and a skilful balance between preserving biodiversity within rapidly developing landscapes.

Key words: behavioural responses; drones; endangered species; environmental influences; Gruidae; human disturbance; land-use transformation; monitoring guidelines; nesting success; unmanned aerial systems; wetlands.

Declaration

I, Carmen Rosa Demmer (Student number: 14771373), declare that this Masters dissertation ("Improving monitoring methods and determining the breeding success of Grey Crowned Cranes, *Balearica regulorum*, within a key agricultural area in South Africa") is my own work and that all the sources that I have used or quoted have been indicated and acknowledged by means of complete references.

I further declare that I submitted the dissertation to the appropriate originality checking software system which is endorsed by UNISA and that it falls within the accepted requirements for originality.

I further declare that I have not previously submitted this work, or part of it, for examination at UNISA for another qualification or at any other higher education institution.

Demmer

Signed: Carmen Rosa Demmer

Date: 14 December 2023

Dedication

“Be strong and courageous. Do not be frightened, and do not be dismayed,

for the Lord your God is with you wherever you go.” - **Joshua 1:9**

For Stuart, my husband, who without hesitation,

always stands by my side.

Preface and disclaimer

The candidate conducted this research as part of her academic pursuits within the Discipline of Zoology, Department of Life Sciences and Consumer Sciences, College of Agriculture and Environmental Science, University of South Africa, Pretoria, South Africa. The research was carried out under the guidance of Associate Professor Trevor McIntyre. None of the material presented in this dissertation has been previously submitted to or considered by any other university. The results documented in this dissertation are solely the outcome of the candidate's investigations. As a disclaimer, we would like to highlight that Chapters 2 and 3 were written as individual papers. This may result in some repetition in a few sections (e.g., methods) between Chapters 2 and 3.

Demmer

Carmen Rosa Demmer (nee Ortmann)

Associate Professor Trevor McIntyre

📷 Carmen Demmer – published on the Getaway Magazine’s feed, 2022.

“Golden Grey Crowned Cranes with a storm rolling in at sunset. This photograph, and this flock in particular, hold much significance to me as it represents individuals from the flock that initially encouraged me to do my research project on this species. It is also when my love for the cranes first took flight.”

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The outputs of this dissertation would not have been possible without the many who generously dedicated their time, energy, financial assistance, guidance, and words of encouragement.

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My acknowledgements would not be complete without thanking my friends and family. Each of you has offered a listening ear, understanding, and moral support throughout my academic journey. The greatest gift I received from my parents has been their support for my passions and interests. Because of you, I had the privilege of extensively travelling our beautiful country when I was younger. I remember the many biodiverse areas we visited with fond memories and appreciate how these holidays instilled and grew my love for nature and conservation. Stuart, words cannot describe your steadfast love, support, and encouragement – not only over the past two years, but this was already evident when we first met. Once again, I am reminded that with you by my side, we can make it through all the hills and valleys of life.

Finally, I give all glory to God, who faithfully guides my steps according to His plan for my life. During the many hours I spent in the field, I was constantly amazed at the complexity and purpose of each aspect in an ecosystem. This only boasts our Creator, the One who gave life to us and all the beauty that surrounds us.

Table of Contents

List of Figures

List of Tables

List of Abbreviations

AIC – Akaike information criterion

G – grams

GCC – Grey Crowned Crane

H – hours

Kg – kilograms

KZN – KwaZulu-Natal

KZNCF – The KwaZulu-Natal Crane Foundation

M – meters

Mm – millimetres

Min – minutes

Sec – seconds

Chapter 1: Introduction

1.1 Title

Improving monitoring methods and determining the breeding success of Grey Crowned Cranes (*Balearica regulorum*) within a key agricultural area in South Africa

1.2 Brief taxonomy and description of focal species

Cranes (Aves: Gruidae) are long-lived species with an average generation length of 12.5 years (Bird et al., 2020). These waterbirds are usually monogamous, physically large, long-legged and -necked. They are found on all continents except Antarctica and South America (Johnsgard, 1983; Krajewski et al., 2010). Four of the fifteen crane species within the Gruidae bird family are endemic to Africa, among them the Grey Crowned Crane, which is the focal species of this study. Grey Crowned Cranes and Black Crowned Cranes (*Balearica pavonina*) are among the oldest species within the crane family, and they are the only two species belonging to the sub-family Balearicinae. The gene pool of Crowned Cranes is split into two sub-species: the Eastern African Grey Crowned Crane (*B. regulorum gibbericeps*), which has a larger

Figure 1.1: Photograph of an adult Grey Crowned Crane (📷 : Carmen Demmer).

area of bare red skin above the white cheek patch, and the Southern African Grey Crowned Crane (*B. regulorum regulorum,* hereafter GCC) (Figure 1.1) (Beilfuss et al., 2007). Grey Crowned Crane adults (which live up to 20 – 30 years in the wild – Allan, 1996; Wamiti et al., 2021) are easily recognisable by their above-average height (± 1 m), grey body feathers, white circular shape on their closed wings, red gular sack under the chin, and characteristic crown of stiff golden feathers (Johnsgard, 1983). Other than their characteristic crown, Crowned Cranes differ from the sub-family Gruine as they have a short, uncoiled trachea which allows them to produce a distinct honking noise (Johnsgard, 1983), and they possess hind toes which enable them to grasp onto structures for roosting or perching (Olupot, 2016). Their taxonomic classification is as follows:

Conservation status: Endangered
Domain: Eukaryota
Kingdom: Animalia
Phylum: Chordata
Class: Aves
Order: Gruiformes
Family: Gruidae
Sub-family: Balearicinae
Genus: *Balearica*
Species: *B. regulorum*

Grey Crowned Cranes were considered Africa’s most common crane in 2004, with an estimated population of 50 000 – 64 000 individuals (Beilfuss et al., 2007). Since then, their population has declined by about 65 – 79 %, which resulted in their up-listing from Vulnerable to Endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (hereafter “IUCN Red List”) in 2012 (BirdLife International, 2024b). The two primary causes of their decline include the destruction and fragmentation of their habitat which has resulted in greater exposure to human pressures and secondly, the illegal removal of birds and their eggs from their natural surroundings (Meine & Archibald, 1996; Olupot et al., 2010; Fakarayi et al., 2016).

1.3 Background

Globally, biodiversity and economic growth compete for the same resources (Olupot, 2016; Tilman et al., 2017), but with economic development progressing at a faster rate, habitat loss and species decline have been on the rise (Stevens & Conway, 2020). Although agricultural landscapes can promote biodiversity (Tyrrell et al., 2020), intensive farming practices commonly drive the transformation of important natural ecosystems, which may negatively affect species diversity (Zedler, 2003). Wetlands are key natural systems that provide unique ecosystem services and habitats for numerous threatened and habitat-specialist species (Donnelly et al., 2022; Hemminger et al., 2022). These ecosystems are vulnerable to intensive agricultural practices such as damming, draining and cultivation, which change their structure and functioning (Sievers et al., 2018; Xu et al., 2019). This, in turn, affects wetland inhabitants when requirements for specific life events become mismatched from the resources provided by the ecosystem (Both et al., 2006; Visser et al., 2015). The cascading effects resulting from modifications to natural ecosystems, together with the loss of habitat specialists, results in a positive feedback loop, causing the loss of fundamental ecosystem functions and services provided by both biotic and abiotic elements (Thackeray et al., 2010; Sievers et al., 2018; Toussaint et al., 2021). Breaking this positive feedback loop by maintaining or encouraging biodiversity could help prevent further function loss (Tilman et al., 2014).

Effectively monitoring and conserving an entire habitat or ecosystem is resource-intensive and challenging, especially when funding is limited (Tyrrell et al., 2020). However, the grave consequences of ecosystem destruction on both humanity and biodiversity have increased global concern and efforts to better maintain and conserve remaining ecosystems and biodiversity (Oliver et al., 2015; Xu et al., 2019; Howard et al., 2020). A commonly employed strategy has been to identify and conserve a particular charismatic species that relies on the habitat in question (i.e., a flagship or indicator species, Murali et al., 2021). The expected outcome is that successfully conserving the charismatic species will also benefit and sustain other community members and overall ecosystem functioning (Toussaint et al., 2021). Cranes (Gruidae) are among the world’s most ancient and threatened avian families (Beilfuss et al., 2007; Krajewski et al., 2010; Harris & Mirande, 2013). Their cultural value and charismatic features have resulted in their use as flagship species to encourage the conservation of natural grasslands and wetlands, thereby also benefiting other species within these habitats (Kanyamibwa, 1993; Marcelino et al., 2020; Fraixedas et al., 2020).

Three of the fifteen extant crane species inhabit southern Africa. The Blue Crane (*Anthropoides paradiseus*) is near endemic to South Africa, occupying a small geographical range in largely grassland ecosystems (BirdLife International, 2024a), while the Wattled Crane (*Bugeranus carunculatus*) is more dependent on wetlands (McCann & Benn, 2006; Altwegg & Anderson, 2009). Grey Crowned Cranes rely on wetlands largely for breeding and grasslands for foraging (Harris & Mirande, 2013; Austin et al., 2018). Although cranes are considered habitat specialists, numerous species are known to benefit from using agricultural land for foraging (Nowald et al., 2018; van Niekerk, 2018; Wamiti et al., 2021). For example, van Velden et al., (2017) report an increase in the survival rates of Blue Cranes in regions where grain crops are grown compared with intact natural habitats. Yet, Su and Zou, (2012) found that Red-crowned Crane (*Grus japonensis*) populations decrease following wetland draining and degradation, since the latter results in a loss of breeding sites. While cranes may attempt to adapt to landscape changes, farmer-crane conflicts continue to increase (Olupot et al., 2010; van Niekerk, 2018). As predictions highlight an increase in land transformation in sub-Saharan Africa in the coming decades (Tilman et al., 2017), there appears to be no end in sight for this conflict. This is particularly concerning for the GCC, sub-Saharan Africa’s most threatened crane species (Harris & Mirande, 2013).

Since the GCC occupies a mixture of grassland-wetland ecosystems and is closely associated with agricultural lands, they are a potentially interesting indicator species for monitoring agricultural impacts on wetlands in the eastern parts of sub-Saharan Africa. Monitoring birds for conservation purposes has been a longstanding practice (Nichols & Williams, 2006; Greenwood, 2007; Neate-Clegg et al., 2020). However, on-foot monitoring of birds that utilise difficult-to-access habitats such as wetlands (one of the primary habitats of the GCCs) poses various challenges in collecting key data metrics when solely reliant on such traditional monitoring methods (Wen et al., 2021; Galloway-Griesel et al., 2022). This has been a major hinderance in informing conservation strategies to safeguard the remainder of this crane species’ population (Linchant et al., 2015). While human population growth and economic development are inevitable, careful monitoring and conservation programmes need to be implemented to cater for this growth and development while ensuring the stability and preservation of the earth’s natural ecosystems and biodiversity (Oliver et al., 2015;

Tilman et al., 2017; Grêt-Regamey et al., 2019; Lavorel et al., 2020).

1.4 Literature review

The present human population growth trajectory is stimulating demand for natural resources at an unprecedented rate (Rawat & Agarwal, 2015; Tilman et al., 2017), resulting in substantial transformation of natural ecosystems to agricultural land-use types. Although this poses numerous impacts on the environment, among the most important is the reduction of habitats through increased fragmentation, significantly impacting biodiversity loss (Drouilly et al., 2018). Grasslands and wetlands are two of the main habitats identified for agricultural development, as these habitats already have optimum conditions for cereal crops and water storage for irrigation (Olupot et al., 2010; Austin et al., 2018). Although landowners can benefit from increased agricultural production when foraging birds assist in pest control, birds can also cause losses by consuming fruits and grains (Anderson et al., 2013; Peisley et al., 2015; Nilsson et al., 2019).

Cranes exhibit both positive and negative responses to agricultural expansion and intensification (Austin et al., 2018). For example, the conservation success of some crane species (e.g., Sandhill Cranes *Antigone canadensis tabida,* and Common Cranes *Grus grus*) should, in part, be attributed to increased agricultural developments (Hemminger et al., 2022). However, GCCs have a specialised life history requiring wetland areas for breeding and grassland habitats for foraging, and unlike many other crane species, they do not migrate (Amulike et al., 2020), although they are known to make periodic local movements in response to food availability and rainfall patterns (Pomeroy, 1980). These life history strategies make the GCC susceptible to disturbances on multiple fronts, likely contributing to their up-listing from Vulnerable to Endangered in 2012. Yet, the habitat preferences of cranes need to be better understood by landowners so that changes to natural habitats do not interfere with the success of crane populations (Fakarayi et al., 2016). While greater awareness is vital, we need to overcome the primary challenge of data scarcity through effective and consistent monitoring and data collection.

To better understand the GCC's response to increasingly developed agroecosystems, this literature review aimed to contextualise and identify essential knowledge gaps, with greater emphasis on the GCC's breeding and habitat requirements. Secondly, I contextualised data collection and monitoring challenges that may impede the effective conservation of wetland-dependent bird species by detailing prior and recent monitoring developments. And lastly, building on the ideas developed from the previous two aims, I suggest possible improvements to traditional monitoring methods to address the growing data paucity concerning GCCs and other large, threatened wetland breeding birds.

1.4.1 Conservation status and distribution of South Africa's crane species

Safeguarding biodiversity has been a global objective, yet population declines and extinction remain a grim reality (Both et al., 2006; Ceballos et al., 2017; Howard et al., 2020). Major land transformations for agricultural development appear inevitable (e.g., sub-Saharan Africa is predicted to undergo prolific agricultural development to support a growing human population – Tilman et al., 2017), however, agricultural lands will remain a key biodiversity pool as numerous species are found in these landscapes in preference to protected areas (Tyrrell et al. 2020). South Africa is considered an internationally important conservation site for the Blue, Wattled, and Grey Crowned Crane (GCC), where these species are primarily reliant on unprotected grasslands and wetlands (Fakarayi et al., 2016; Galloway-Griesel et al., 2022). KwaZulu-Natal (KZN), one of the few provinces supporting all three crane species, has already seen major transformations of these natural habitats into plantations, pastures, and croplands (Morrison & Bothma, 1998; Weyer et al., 2015). The reliance of cranes on these vulnerable habitats, together with their slow reproductive rate, generally small clutch sizes, and extended parental care, all contribute to a greater extinction risk of these birds (Owens & Bennett, 2000; Simmons et al., 2004; Toussaint et al., 2021).

Species decline and aspects affecting their decline are bound to differ between regions (Ceballos et al., 2017). This means that conservation strategies employed in one region or on a particular species may not work for another elsewhere. Eleven of the 15 extant crane species are categorised as threatened (Beilfuss et al., 2007), primarily because of habitat loss. The sensitivity of cranes in response to changes in their environment has highlighted their ecological importance as indicator species (Kanyamibwa, 1993; Harris & Mirande, 2013; Han et al., 2018; Nováková & Robovský, 2021). Uncommon or rare species have been shown to contribute novel and distinct functions towards ecosystems, emphasising their importance for conservation strategies (Mouillot et al., 2013). Because of this, several authors argue that functional diversity is a more practical measure of ecosystem health (Rawat & Agarwal, 2015;

Toussaint et al., 2021). Yet, ecological theories such as the mass-ratio hypothesis downplay the importance of less abundant species (e.g., the Blue Crane and GCC) because of their low contribution to biomass (Grime, 1998). To overcome these conflicting views, others have viewed species richness as a measure of ecosystem health and rare species as an insurance for ecosystem functionality; however, this still downplays the importance of rare species in providing novel functions. As such, rare, functionally distinct species should be given higher priority in conservation programmes (Both et al., 2006; Thackeray et al., 2010; Mouillot et al., 2013; Charmantier & Gienapp, 2014). Altogether, this suggests that maintaining endemism and increasing focus on smaller-ranging species (i.e., most threatened species) with unique ecological functions may help preserve the biodiversity in smaller hotspots, ultimately assisting in improving biodiversity at a larger scale (Murali et al., 2021). Whilst cranes may be useful in such a conservation approach, significant knowledge gaps still exist in our understanding of these birds.

Blue and Wattled Cranes have been relatively well-studied, and in recent years, their IUCN Red List rating has been down-listed to “Vulnerable” following stable population trends (Harris & Mirande, 2013; Olupot, 2016; Galloway-Griesel et al., 2022; Wamiti et al., 2022). Although Galloway-Griesel et al. (2022) indicate greater stability of the current number of GCCs in KwaZulu-Natal, their numbers are still declining elsewhere. They were up-listed from Vulnerable to Endangered in 2012 following a significant (30 – 49 %) decline in their global population over recent decades (Morrison, 2015; Morrison et al., 2019). With their natural habitats increasingly shifting towards human-dominated landscapes, GCCs have experienced increased incidences of poisoning, breeding failures following damming and drainage of wetlands, powerline collisions, hunting, illegal trading, disease, and predation (Harris & Mirande, 2013; Olupot, 2016; Amulike et al., 2020; Galloway-Griesel et al., 2022). Furthermore, a poor understanding of this species’ breeding success, nest site preferences, and habitat availability have hindered effective conservation (Fakarayi et al., 2016; Wamiti et al., 2022) – especially in response to increased anthropogenic presence. This species’ vulnerability to habitat loss highlights the need to assess their historical and present breeding status and habitat utilisation to assist in developing baselines and addressing data paucity (Stevens & Conway, 2020). Given the close associations of GCCs with wetland areas for breeding, their risk of extinction may increase unless they can readily adapt to a changing environment (Wamiti et al., 2022).

1.4.2 Breeding biology, nest site selection, and breeding success

Breeding biology

Before becoming sexually mature, juveniles generally travel further than adults to locate new foraging grounds and mating opportunities, thereby acting as a form of dispersal (Wolfson et al., 2020; Thompson et al., 2022). Conversely, adults (specifically of non-migratory crane species) tend to undertake shorter movements to defend territory and raise young. Most crane species are highly social and gather in medium (n >= 30) to large (n >= 150) “floater flocks” during their non-breeding season (Miller & Barzen, 2016; Austin et al., 2018; Ojaste et al., 2020; Galloway-Griesel et al., 2022). These floater flocks provide interaction opportunities among individuals and allow immature cranes to identify a suitable mate. During flocking periods, cranes are often seen displaying in the form of a dance, a behaviour that improves bonding or pairing up for the next breeding season. Whooping Crane (*Grus americana*) breeding pairs begin associating some years before commencing breeding and even before reaching sexual maturity (Teitelbaum et al., 2017). Comparable findings have been noted in a marked cohort of GCCs at Lake Ol’ Bolossat in Kenya, where pairs had formed at approximately two years of age and, under favourable conditions, started breeding at around five years of age (Wamiti, pers. Obs., 2024). This close association may have some post-breeding benefits with greater familiarity between partners reducing the chance of separation and thus improving parenting ability. These findings highlight the valuable role of these flocking periods in the reproductive success of these species and perhaps cranes in general.

After reaching sexual maturity between four and six years, GCC pairs associate and become highly territorial during their breeding season, often then mating for life (Pomeroy, 1980; Morrison, 2015; Wamiti et al., 2022). Crowned Cranes generally nest during the wet season (Geldenhuys, 1984; Sundar, 2009; Wu et al., 2009; Hayes & Barzen, 2016). In South Africa, the peak egg-laying period of GCCs occurs between November and January; however, in other geographical regions such as Kenya, this species breeds all year round (Morrison, 2015; Wamiti et al., 2022). Breeding during higher rainfall allows them to take advantage of the greater seed and insect abundance to ensure good chick growth and parent condition (Gichuki, 2000; Austin et al., 2018; Wamiti et al., 2022). Grey Crowned Cranes construct large platform nests amongst the tall, damp vegetation in wetlands (Wamiti et al., 2020). This helps to conceal the nest and their young from land predators (e.g., serval *Leptailurus serval*, and black-backed jackal *Lupulella mesomelas*). Another strategy employed by GCC parents is synchronised incubation, whereby both parents share incubation responsibilities to protect eggs from aerial predators (Wamiti et al., 2020; Wen et al., 2021).

Grey Crowned Cranes are among the smallest crane species, yet their clutch sizes are larger (*n* = 2 – 3 and rarely 4 eggs) than those of other cranes (Wamiti et al., 2022). They also attempt to rear all hatchlings in a season rather than selecting to raise just one of their offspring (e.g., Wattled Crane) (Morrison, 2015; Zelelew et al., 2019). Other species, such as the Blue, Whooping and Sarus (*Grus antigone*) Cranes, also lay multiple eggs (*n* = 2) and attempt to rear both offspring; however, only one offspring generally survives (Bidwell, 2004; Sundar & Choudhury, 2005). Egg manipulation can be an effective conservation tool, especially when more than one egg is laid. For example, removing Whooping Crane eggs during incubation can improve overall nest success by rearing captive young whilst allowing parents to provide increased attention to a single offspring (Boyce et al., 2005). As with other crane species, GCC parents share responsibilities throughout their (28 – 31 days) incubation period (e.g., Sundar & Choudhury, 2005; Zhang et al., 2017) and during chick rearing. Following hatching, parents teach their offspring foraging skills and anti-predator behaviours. The GCC's anti-predator behaviours usually take the form of hiding their chicks, leaving the area to divert attention from the nest or offspring, and returning only once it is safe to do so (Morrison & Bothma, 1998). Combined parental care allows young cranes to spend more time foraging while parents remain vigilant (Alonso & Alonso, 1993; Hartup & Horwich, 1994; Nowald, 2001). Once GCC chicks fledge (55 – 100 days after hatching – Gichuki, 2000), parents and their sub-adult offspring usually join nearby floater flocks for the non-breeding season. The adult pair then returns to their breeding site in the following season to reinitiate breeding, leaving their offspring from the previous season in the floater flock (Johnsgard, 1983; Morrison, 1998).

Longer-lived species display a delayed life-history curve where reproductive output tapers off as they reach senescence (Brown & Orians, 1970; Ekman et al., 2004; Hammers et al., 2012; Barwisch et al., 2022). This general pattern also holds true for cranes. Members belonging to the crane family display generational lengths of approximately 12 years, which is substantially longer than the average of about three years for all bird species (Owens & Bennett, 2000; Zelelew et al., 2019; Bird et al., 2020; Edwards et al., 2022). However, the delayed sexual maturity of juvenile cranes (Tacha et al., 1989; Coverdale & McCann, 2003; Brown et al., 2019) is a major limiting factor of successful crane conservation efforts (Donaldson et al., 2023). Identifying reproductive metrics and the factors that inhibit or promote reproductive success is therefore key to ensuring successful conservation outcomes, especially in long-lived species such as cranes (Nisbet, 2001; Wamiti et al., 2022).

Nest site selection

Cranes usually show a strong separation in their breeding and foraging habitats. While foraging habitats are fairly exposed, their breeding site choice is more conservative, with most crane species nesting at higher altitude sites and wetlands (Morrison & Bothma, 1998; Borad et al., 2001; Wu et al., 2009; Han et al., 2017). A significant challenge in crane conservation is the declining availability of these sites within intensively farmed landscapes (Beilfuss et al., 2007). Grey Crowned Cranes may be more vulnerable to changes in their environment because of their non-migratory behaviour and life-history traits, which may limit long-distance movements in search of alternative foraging and nesting sites during harsh periods (Ramírez et al., 2018; Donnelly et al., 2022; Wamiti et al., 2022). In some regions GCCs avoid nesting near disturbed wetlands (Morrison & Bothma, 1998), but over the subsequent decade there were increased reports of GCCs utilising disturbed waterbodies (Olupot et al., 2010). Although this may suggest some adaptation of GCCs to changes in their environment, more frequent nesting in human-modified habitats does not necessarily translate into successful breeding outcomes. Disturbances to vulnerable breeding habitats generally affect the environmental factors surrounding the breeding site, which can directly or indirectly influence a species' reproductive success (e.g., Wu et al., 2009; Zhang, An, Shu, & Yang, 2017; Wamiti et al., 2022).

Spatial scale and environmental factors (e.g., disturbances from nearby settlements and roads, water body proximity, vegetation height and density) are known to influence the White-naped Crane's (*Grus vipio*) perception of habitat availability and nest site suitability (Wu et al., 2014). Like White-naped Cranes, GCCs also tend to select nest sites that are associated with tall vegetation (Morrison & Bothma, 1998), while water depth and distances to open water edges further influence the likelihood of nest sites being located in specific areas (Wamiti et al., 2020; Wamiti et al., 2022). These micro-habitat characteristics can influence the survival of young by improving egg and chick protection, modifying the physical conditions around the nest (e.g., temperature and humidity) that affect egg development, or reducing the distance to food sources (Wu et al., 2014). Although cranes seldom re-use the same nest for subsequent breeding attempts, successfully raising young at a nest site may increase the likelihood of a pair returning to the same wetland or waterbody in the following breeding season (Morrison, 2015).

An alternative explanation for increased nesting in disturbed locations might be that cranes have little choice but to select nest sites in these areas since preferred sites have become saturated (Fox et al., 2019). Yet a greater understanding is needed of GCC nesting requirements and the resilience and adaptation of their breeding strategies in response to particular land-use types. One tool that may be useful in this regard is a species/habitat distribution model (Franklin, 2013). Species/habitat models already exist for some crane species in specific regions (Han et al., 2017; Mi et al., 2017; Zacarias, 2018) and for GCCs in Uganda (Stabach et al., 2009) but they do not yet exist for GCCs in KZN. Assembling such a model could greatly assist with predicting the future habitat availability and survival rates of GCCs in response to climatic and land-use projections in the southern Drakensberg – an internationally important site for crane conservation (Galloway-Griesel et al., 2022). If GCCs can breed in urban or disturbed wetlands successfully, this could sustain their population sizes, as is seen with the well-adapted Sarus, Demoiselle (*Grus virgo*), and Sandhill Cranes (Fox et al., 2019; Zelelew et al., 2021).

Breeding success

A species' ability to breed and successfully raise young positively contributes to the stability of its population (Caswell, 2000; Crone, 2001; Kerr, 2020). Since hatching failure is a common challenge amongst threatened bird species (Assersohn et al., 2021), improving reproductive output is a fundamental component of successful conservation programmes (e.g., Ekman et al., 2004; Lacy et al., 2015). Several key reproductive metrics require consideration for a general understanding of a species' life history (e.g., egg success, nest success – Murray, 2000) and to inform conservation decisions (age at first reproduction – Nisbet, 2001). Breeding programmes attempt to assist in this aspect by raising young in a captive setting for re-introduction into the wild (Jones et al., 1995; Bowkett, 2009; Bussolini et al., 2023). Such programmes have commonly been trialled for crane species, but population recovery has not been consistently successful (Coverdale & McCann, 2003; Beilfuss et al., 2007; Edwards et al., 2022; Thompson et al., 2022; Donaldson et al., 2023). This is mainly because of challenges relating to offspring viability and the extended period required to reach sexual maturity.

The finer details of GCC breeding success, specifically concerning the influences of environmental conditions, are largely unknown. Previous related research on GCCs investigated some of these metrics, but conclusions were largely unsuccessful. This has been because of challenges in locating nest sites and difficulties in monitoring nests from eggs through to fledglings (metrics required for determining comprehensive breeding success) (Morrison, 1998). Nonetheless, their research provided measures of GCC average clutch sizes, reportedly the largest (approximately 2.5 eggs) of all crane species (Morrison, 1998). This species' preference for tall vegetation could also make nest sites vulnerable to intensive grazing since this could affect the nest's structural integrity and may expose the nest to predators (Olupot et al., 2010). On the other hand, moderate grazing around GCC nest sites could be beneficial, as grazing animals attract insects (e.g., dung attracts soil invertebrates while new plant growth and greater plant species richness resulting from large grazing herbivores has shown to increase grasshopper abundance – Zhu et al., 2012) and deter domestic predators such as dogs and cats (Gichuki, 1993). Furthermore, geographic variation in the probability of breeding success may be associated with latitude. Since GCCs can breed over extended periods in the mid and southern latitudes, this allows more opportunity to renest if a nest fails early in the season (Meine & Archibald, 1996).

Grey Crowned Crane breeding success in South Africa was previously reported as a 100 % hatching rate (likely over-estimated) and a fledging rate of 42.5 % (McCann & Wilkins, 1995), whilst later reports from Kenya suggested hatching rates of 94.3 % and fledging rates of 67.3 % (Gichuki, 1996). Fledging mortality rates during the first year for GCCs in KZN were estimated to be 35.3 %, dropping by 7.2 % in subsequent years (McCann & Wilkins, 1995). Low fledging rates and substantial declines in GCC populations have heightened the urgency of conservation efforts to ensure the sustainability of this species (Beilfuss et al., 2007). While historical breeding metrics may provide some insight into this species' breeding success in previously intact and untransformed habitats, updated and current metrics may be even more concerning than previously predicted.

Figure 1.2: A Grey Crowned Crane with two chicks walking in a dairy pasture in southern KwaZulu-Natal, South Africa (📷 : Carmen Demmer).

1.4.3 Wetland bird monitoring for conservation

To maintain biodiversity and ecosystem functioning, ecologists and conservationists should prioritise effective and accurate data collection through regular monitoring to best inform conservation decisions of extant species (Znidersic, 2017; Robinson et al., 2018). To achieve this, they need to consider the cost-effectiveness of projects, potential limitations of ecological tools, and the characteristics of the focal species (i.e., abundance, visibility, and habitat type or range of the species) before implementing data collection or monitoring (Singh & Milner-Gulland, 2011; Trolliet et al., 2014). Conventional sampling and observational methods may be adequate for abundant and conspicuous species that inhabit open vegetation (Belton et al., 2018; Qufa & Bekele, 2019; Rime et al., 2020). However, alternative methods are required for optimal data collection for rare or inconspicuous species that inhabit logistically challenging environments (Znidersic, 2017; Schad & Fischer, 2022). This section outlines the challenges surrounding data collection at breeding sites of uncommon waterbirds with specific reference to the GCC. It also discusses the advantages and disadvantages of traditional and novel monitoring methods, whilst identifying present and future technologies that could improve data collection and the impact of this information on existing conservation programmes.

Grey Crowned Cranes mostly forage and socialise in grasslands and croplands (Stabach et al., 2009; Fakarayi et al., 2016). Monitoring cranes and other large birds under these conditions with traditional methods can be relatively simple, with researchers generally employing spotting scopes and aerial photography to monitor their behaviour and to count individuals (Reintsma et al., 2018; Galloway-Griesel et al., 2022). But, as already highlighted, GCCs nest among tall reeds in wetlands and other inland water bodies. This makes their nest sites challenging to locate and monitor (Wamiti et al., 2020; Wen et al., 2021). Collecting breeding metrics is important for informing targeted aspects of conservation management through a better understanding of variables that may influence a species' nest site selection and breeding success (Conover et al., 2011; Assandri et al., 2017; Wamiti et al., 2020). As such, valuable data have been obtained to date by accessing wetland nest sites via wading or boating, thereby physically measuring nest site factors (involving invasive procedures such as close proximity to birds on nests and handling of eggs) (Ruiz-Guerra & Echeverry-Galvis, 2019; Zelelew et al., 2019). Despite the value of this information, collecting data in this manner creates pathways to nest sites – which make nesting birds more vulnerable to natural predators, whilst disturbances to nesting birds may result in nest abandonment and reduced chick survival rates (Coverdale, 2006; Champagnon et al., 2019; Wamiti et al., 2020). In KZN, these challenges are partially overcome by monitoring crane populations and breeding sites through aerial surveys using aeroplanes (Galloway-Griesel et al., 2022). While this method can monitor population trends of the focal species, aerial monitoring in KZN is limited to annual flights during the non-breeding season of the GCC. This is primarily because of the high costs involved in implementing this monitoring method, which would rise significantly if extended to monitoring the breeding periods of the other two local crane species (Galloway-Griesel et al., 2022). Effective and regular monitoring of the focal species' breeding via traditional methods has thus remained challenging (on-foot methods) and is virtually non-existent (aerial surveys).

1.4.4 Technology overview

Traditional methods

Marshland and wetland birds have been, and still are, often detected by their vocalisations, while monitoring relies primarily on presence/absence estimates through direct observations, bioacoustic techniques, and call-playbacks of birds (Nasirwa &

Bennun, 2000; Conway, 2011; Frommolt & Tauchert, 2014; Frommolt, 2017). These traditional methods may be cost-effective, but they are also time-consuming and easily biased by external factors such as the distance of the birds to the caller, vegetation density, and weather conditions (Conway & Gibbs, 2011; Verhoeven et al., 2020). On-foot methods are valuable for dry terrain (when the focal species is abundant and less sensitive); however, covering larger areas may become less effective and more resource-intensive (Francis et al., 2020). Aeroplanes have thus long been employed as a monitoring tool to help gather data in logistically challenging habitats, such as wetlands (Kingsford & Porter, 2009; Galloway-Griesel et al., 2022). Aerial surveys are useful to determine a species' density, and large areas can be quickly covered over a short period. This minimises the chance of detecting a bird or flock multiple times – as might occur when observations take place over weeks or months (Kingsford & Porter, 2009). Furthermore, aerial photographs provide a lasting data record that can be used for subsequent *post-hoc* data analysis allowing for exact counts of individuals, which, if repeated annually, can provide comprehensive population trends (Galloway-Griesel et al., 2022). However, this method is costly (Anderson & Gaston, 2013) and vulnerable to biases or errors relating to species size and reaction to aerial threats and noise, weather conditions, and vegetation cover (thus limited to larger-sized animals, open habitats, and clear weather, flight path, aircraft type and observers' ability and fatigue) (Hedges & O'Brien, 2012). Although traditional methods mentioned earlier facilitate interaction with community members and volunteers, some argue that using aerial surveys reduces such opportunities for community engagement (Wamiti & Kimani, 2020).

Another challenge in monitoring birds is identifying an individual's movement through an area or across the globe. Although aerial surveys may provide a snapshot of a species' distribution throughout an area, it is challenging to determine which habitats are preferred at the individual level. Bird rings can be used as an alternative to obtain such behavioural and ecological information (Webster et al., 2002; Anderson & Green, 2009; Thorup et al., 2014). Rings are generally placed on a bird's leg from fledging onwards, with combinations of numbers and colours used to identify individuals, and recorded morphological measurements describe the ringed subject (Griesser et al., 2012). Ringing is relatively cost-effective, but it does require regular monitoring and a substantial number of ringed individuals to improve the chances of finding a ringed bird during subsequent observations, which can be time-consuming (van Velden et al., 2017). However, this method has proven useful in East Africa (specifically Kenya and

Uganda), where an ongoing programme for ringing crane juveniles not only identifies individual birds but also populations through selected colour ring combinations (Wamiti, pers. comm., 2024). This methodology has also been implemented on some crane species in KZN (Morrison, 1998; McCann & Benn, 2006; van Velden et al., 2017). One of these studies (van Velden et al., 2017), reported ringing 649 Blue Cranes and obtained valuable course-scale insights into Blue Crane movement patterns. However, they suggested using alternative methods (e.g., animal-borne GPS (Global Positioning System) tags) to improve post-tagging collection efficiency and to provide a more robust and accurate understanding of fine-scale movement patterns of this species. Despite the accuracy and potentially high spatio-temporal frequency of rings, there is always a risk of physically harming the bird by selecting an incorrectly sized ring, which can result in inflammation or crippling of the leg (Griesser et al., 2012). These traditional approaches have provided substantial data and insight into bird population dynamics and ecosystem functioning. But there are certainly costs (in the form of financial, physical handling and disturbance) associated with these methods that could be overcome through newer technologies and methods.

Novel methods

The many possible limitations experienced through direct observations, aerial surveys, and ringing or tagging can, to some extent, be overcome by adopting newer technologies – often providing more effective and efficient data collection than direct methods (Fiedler, 2009; Verstraeten et al., 2010; Hodgson et al., 2016, 2018; Lee et al., 2019). More advanced methods used to monitor rare and inconspicuous species found in challenging terrain include camera traps, animal-borne tags (including high frequency, GPS, and satellite-linked tags), and use of unmanned aerial vehicles (UAV) commonly known as drones (Vas et al., 2015; Borrelle & Fletcher, 2017; Lyons et al., 2018; Afán et al., 2018; Francis et al., 2020; Wen et al., 2021; Wilson et al., 2021). Animal-borne tags provide more detailed information on waterbird movement patterns and habitat utilisation and reduce the amount of time required to directly monitor the subject (e.g., Sandhill Cranes – Donnelly et al., 2021; ducks – McDuie et al., 2019). However, these tracking devices can impede a bird’s locomotive ability, increase the time spent foraging, and raise divorce rates, which may reduce the chance of nesting (Culik et al., 1994; Barron et al., 2010; Bodey et al., 2018; Lameris et al., 2018). To minimise this impact on an animal’s locomotor ability (especially swimming or flying animals), researchers have been encouraged to optimise the tag design and positioning on the animal by using computational fluid dynamics. Doing so has shown to reduce the drag imposed by a generic tag on seals by up to 22 % (Kay et al., 2019). Attaching GPS tracking devices is more complicated than ringing, which prolong the handling process and causes greater stress on the subject, potentially resulting in death (Barron et al., 2010). While this approach may be costly, advancements in technology aimed at reducing the size and enhancing the suitability of devices for specific target species are expected to decrease the costs associated with deploying these devices (Kay et al., 2019).

Camera trapping is another monitoring method that has been successfully implemented for detecting rare, cryptic, and nocturnal animals – often being used to study the abundance, density, and behaviour of wildlife (Trolliet et al., 2014; Swanson et al., 2015; Znidersic, 2017; Colyn et al., 2020; Ortmann & Johnson, 2021; Moore et al., 2021; Cordier et al., 2022; Laux et al., 2022). Animals are more likely to display natural behaviour in front of camera traps than in the presence of human researchers (Singh & Milner-Gulland, 2011). Although this is a significant benefit, the initial and recurring monitoring costs may be high as sites need regular visiting to ensure that camera traps are still functioning optimally. For example, researchers must ensure that vegetation has not altered the fields of view of camera traps, Secure Digital cards have not reached their storage capacity (if camera traps do not have transmission capability), batteries are functional, and camera traps have not been stolen or damaged (Singh & Milner-Gulland, 2011). With specific reference to bird monitoring, camera traps have made a significant contribution to research on elusive and rare species (e.g., the White-winged Flufftail *Sarothrura ayresi* – Colyn et al., 2020; and the critically endangered Hooded Vulture *Necrosyrtes monachus* – Fern et al., 2022). Other research has employed this tool to monitor nesting and foraging behaviours, detect predator-prey interactions, and estimate species composition and abundance within a community (Moore et al., 2021; Laux et al., 2022). Camera traps become less effective for research questions beyond this as the number of camera traps needed often becomes excessive (Kays et al., 2020). Extracting data from the resulting images or video clips also becomes more time-consuming, especially when there are many false positives. To overcome this, citizen scientists and machine learning techniques can be used together, to produce a model that can detect empty images and successfully differentiate between mammalian species with a high degree of accuracy (Willi et al., 2019).

The limitations of the methods discussed above seem to outweigh their benefits in relation to the research questions of this study. Aerial surveys are irregular and costly, while positioning camera traps amongst waterlogged vegetation is likely to pose as much disturbance as visiting nest sites on foot. As such, newer technologies might have greater potential. Remotely Piloted Aircraft Systems (hereafter drones) have become increasingly popular, and numerous studies boast their affordability (in comparison to aeroplanes) and versatility in better understanding animal behaviour and population dynamics (Anderson & Gaston, 2013; Ivosevic et al., 2015; Linchant et al., 2015; Han et al., 2017; Wen et al., 2021; Corcoran et al., 2021; Sorrell et al., 2023). Their manoeuvrability and wide field of view have enabled precise counts and accurate identification of breeding populations for both waterbirds and seabirds (Afán et al., 2018; Hodgson et al., 2018; Lyons et al., 2018; Wen et al., 2021). Monitoring and data collection can also be completed more quickly (e.g., Gallego & Sarasola, 2021), thereby improving in-field monitoring effectiveness and potentially reducing the stress experienced by subjects. Furthermore, drone software allows for entire areas to be quickly and systematically mapped, enabling multiple species to be detected remotely without handling subject animals and with minimal disturbance to the surrounding habitat (Christie et al., 2016; Han et al., 2017). Despite the wide-ranging use of drones, Callaghan et al. (2018) stress that drone monitoring should be coupled with traditional fieldwork methods when determining the breeding success of birds, as this promotes a more holistic dataset collection.

Introducing any monitoring tool into an animal's environment will likely introduce at least some disturbance. The noise and unusual movement patterns of drones are no different. Recent studies investigated the response of animals to the presence of drones and revealed that birds are more sensitive to drone monitoring than other vertebrate types (Mulero-Pázmány et al., 2017; Rebolo-Ifrán et al., 2019). However, these responses are species-specific (Vas et al., 2015; Barr et al., 2020; Duporge et al., 2021; Wilson et al., 2021). Presently, no drone monitoring protocols exist for cranes in general or GCCs specifically. Vas et al. (2015) conducted various trials on medium to large waterbirds (mallards *Anas platyrhynchos*, flamingos *Phoenicopterus roseus*, and greenshanks *Tringa nebularia*). The birds in their study showed no significant differences in behavioural response when drones were flown at different speeds, but approach angles were important. Birds were less responsive to diagonal approach angles but showed increased responsiveness indicative of stress when approached at 90° (Vas et al., 2015) or when hovering above birds (Lyons et al., 2017). Generally, data collection benefits from lower drone flight heights, but closer approaches to animal subjects generally also impose greater disturbance (Lyons et al., 2018; Francis et al., 2020; Schad & Fischer, 2022). Therefore, some studies have provided guidelines in this regard, suggesting taking off at specific minimum distances from the area of interest and generally flying at higher altitudes to reduce the probability that animals will attempt to escape (e.g., Weston et al., 2020) (although this behaviour can also be highly species-specific – Barr et al., 2020).

The use of drones for monitoring waterbirds

Drones are typically flown in low-lying airspaces (< 120 m above the ground), potentially influencing visual and acoustic activities of species that utilise this space (Scholten et al., 2020). Despite the increasing number of publications that advocate for using drones in wildlife monitoring, relatively few studies have actively compared disturbance levels between drones and traditional data collection methods. One study approached wading birds on foot and used a range finder to determine the distance from the observer to the birds, recording behavioural changes that may allude to a disturbance effect associated with their approach (Reintsma et al., 2018). Through direct comparisons, their findings concluded that drones were more efficient and caused less immediate disturbance to wading birds. Similarly, Chinstrap Penguins (*Pygoscelis antarcticus*) responded more negatively to human observers conducting ground surveys than to drones flying 30 m above them (Krause et al., 2021). Others have also suggested that drones are more effective at collecting data, once again emphasising quicker (and likely less disturbance) data collection with drones than with traditional fieldwork methods (Valle & Scarton, 2020; Gallego & Sarasola, 2021). However, while such studies made inferences about disturbances incurred by the animal subjects when monitored with traditional and drone-based methods, levels of disturbance were not quantified. It is also important to note that immediate responses may not fully describe the overall level of stress experienced by the animal (Zink et al., 2023). For example, Eurasian Oystercatchers (*Haematopus ostralegus*) temporarily abandoned their nests, whether monitored with drones or on-foot methods (Valle & Scarton, 2019). Yet, Oystercatcher parents spent lengthier periods away from their nests when disturbed by drones. These examples show that no single monitoring method is preferred by all species, but the consequence of employing the wrong monitoring method can be severe.

A primary consideration before implementing drones in an environment includes assessing any potentially harmful effects (stress) of using drones on the subject species as well as other surrounding species (by-catch) (Vas et al., 2015; Reintsma et al., 2018). Stress is generally measured through physiological changes such as corticosterone levels or behavioural changes in the subject species (Weimerskirch et al., 2018). Ideally, both behavioural and physiological changes should be measured. However, measuring the latter usually includes physically handling the species to attach internal (e.g., Zebra Finches *Taeniopygia guttatal* – Zagkle et al., 2020) or external data loggers (e.g., sub-Antarctic seabirds – Weimerskirch et al., 2018). Alternatively, blood or tissue samples can also be collected for subsequent analysis which can cause further stress. Assessing associated metabolites from faecal samples is also possible, but measuring metabolites in avian species is complicated – urine and faeces are often excreted simultaneously, leading to unknown proportional estimates of hormones in urine or faeces (Sheriff et al., 2011). It is important to note that physiological changes may either be expressed immediately or may be delayed (Borrelle & Fletcher, 2017). Birds may therefore not physically manifest stress via behavioural cues. Considering drone-based research studies, those that quantify stress experienced by animals generally did so by measuring behavioural changes (Altena & Goedemé, 2014). Behavioural changes can be widely categorised according to the severity of disturbance expressed through behavioural cues, ranging from least to most disturbed (Vas et al., 2015; Brisson-Curadeau et al., 2017; Albores-Barajas et al., 2018; Wen et al., 2021; Fudala & Bialik, 2022). If the target species displays minimal physiological or behavioural changes, particularly when using existing monitoring methods, drones could be trialled as an alternative method for monitoring and data collection of the species (Schad & Fischer, 2022).

In its unprocessed form, data obtained from drone sensors typically consists of images or videos, while further information can be extracted by using post-processing methods. Manual data extraction may be sufficient for smaller studies (e.g., determining the number of individuals in a specific area, species composition, behaviour responses, Tuia et al., 2022). Larger and more complex biogeographic studies that involve measuring distances, areas and extracting location type data will likely require further post-processing in a geographical information system. These larger-scaled monitoring projects may benefit from developing and training classification and object detection models via machine-learning techniques (often used for species abundance counts) to improve their data processing rate (Tuia et al., 2022). Although machine learning techniques are useful, they are not always perfect. The variable nature of the imagery collected by drones in terrestrial systems incurs frequent misidentification of objects since subjects may not be well contrasted from their background or differences between similarly sized and coloured heterospecifics may not be detected (Francis et al., 2020; Schad & Fischer, 2022). The initially time-consuming task of assembling manually annotated datasets to train a model of the target species and the technical ability required to develop a machine learning model can increase the chance of introducing potentially costly mistakes into the data extraction and analysis workflow (Francis et al., 2020). As such, researchers should proceed cautiously with these methods and, where necessary, employ the expertise of those well-versed in these techniques to ensure that the maximal value can be obtained from these data.

Although being a relatively recent development, drones have been employed across a wide variety of species. However, limited research shows the use of drones for monitoring cranes. I found three studies that reported the use of drones for crane research. The earliest of these studies demonstrated the effective use of drones and detection algorithms to count roosting Sandhill Cranes (Stark et al., 2017). While the others determined the abundance of Siberian Cranes (*Leucogeranus leucogeranus*) in China (Wen et al., 2021) and more recently, detecting and counting Common Cranes (Chen et al., 2023). Several studies have attempted to compare the accuracy of drone and ground counts. The findings of Wen et al. (2021) corroborated the results reported by Francis et al. (2020), who used semi-automated means of counting waterbirds and highlighted accuracy rates of > 90 % when using freely available software options. Yet the species-specific nature of using drones requires tailoring guidelines according to the response of a certain species to the possible disturbances emitted by a drone. While the previously stated studies revealed useful information when using drones for research on cranes, no specific guidelines exist for cranes in general, or for GCCs specifically.

1.4.5 Conclusions

Maintaining viable crane populations in globally important conservation sites is crucial to allow for their ongoing persistence and important contributions to ecosystems. Unfortunately, traditional monitoring methods are time-consuming and inefficient, impeding conservation efforts and neglecting the study of crane species that inhabit difficult-to-access areas. Technological advancements have proven useful in obtaining essential information for other endangered species undergoing comparable challenges. Therefore, adopting comparable monitoring methods could improve data collection without causing major disturbances to the target species. This data would be invaluable for future conservation planning and the continued survival of these threatened, wetland nesting crane species.

1.5 The problem statement and justification

The GCC, a charismatic and endangered icon of Africa's wetlands and grasslands (Morrison, 2015), faces population decline due to habitat loss and human disturbance from agricultural expansion. Their dependence on intact ecosystems necessitates prioritizing conservation efforts. However, effective strategies require a deeper understanding of the species' habitat use, behaviour, movement, and ecology. The Drakensberg emerges as a critical site for international crane conservation as all three local crane species reside here (Galloway-Griesel et al., 2022). This biodiversity hotspot faces threats from land-use changes which are impacting key habitat sites of cranes and other endangered species. Studying GCCs in this area would not only inform regional conservation but could also contribute globally by emphasizing the importance of protecting this species and the habitats it relies on. While traditional aerial surveys offer limited data collection during the non-breeding season (Anderson & Gaston, 2013; Galloway-Griesel et al., 2022), on-foot monitoring at nest sites, though valuable for breeding metrics, can disrupt incubation and lead to parental abandonment (Coverdale, 2006; Fakarayi et al., 2016; Harris & Mirande, 2013; Wen et al., 2021). Consequently, inconsistent monitoring and limited knowledge about this species' breeding success, nest site selection, and habitat availability (particularly in KZN) hinder the development of effective conservation plans for this endangered species. Enhancing these methods is essential for data collection and informing future conservation strategies.

1.6 Aims and research questions

Many of the research problems mentioned above stem from the constraints of traditional monitoring techniques. As such, the initial objective of this research was to compare the use of drones and traditional monitoring methods (i.e., on-foot), to determine whether drones could improve the efficiency and accuracy of monitoring and data collection. Provided that drones can be shown to safely and effectively monitor GCC groupings, this study further aimed to utilise drones to identify the breeding success of GCCs in the southern Drakensberg by collecting breeding metrics at nest sites. The data obtained from the second aim could then be used for the last aim, which sets out to describe important macro-environmental factors that influence GCC breeding success. These aims were developed with the intention of answering the following research questions (predictions stated below the questions):

- What are the behavioural responses of GCC social groupings (pairs, families, and flocks) when monitored by on-foot and drone methods?
- Can drones obtain accurate breeding metrics at nest sites without causing major disturbance to breeding pairs and nesting activities? How should drones be used to minimise the disturbance to breeding pairs while collecting breeding metrics from nest sites?
- If drones were used to monitor GCC social groupings, how should the drone be operated (e.g., take-off point, flight height and drone approach angle) to effectively obtain accurate data without disturbing groupings?
- Does overall breeding success of GCCs in the southern Drakensberg align with similar metrics collected in other regions?
- Which macro-environmental factors promote or hinder GCC breeding success and why?
- Do GCCs show a tolerance to human presence and land-use change?

This study therefore aims to investigate the potential of drones as a monitoring tool for GCCs. I hypothesize that drones can be effective, but with varying levels of disturbance, depending on the social grouping type (hypothesis 1). Because of the presence of offspring, I predict that family group types would potentially be more sensitive than others and might exhibit increased calling, flushing, or aggression towards the unfamiliar aerial presence (hypothesis 2). As humans are often viewed as a threat, I hypothesised that on-foot monitoring might elicit similar responses but that drones (which are smaller and may be viewed by a GCC as another bird) would achieve closer approaches (hypothesis 3). When monitoring nest sites that may be vulnerable to aerial predators, I hypothesised that drone flights that mimic the behaviour or aerial predators will increase the flight chance of nesting birds (hypothesis 4). Although GCCs exhibit some tolerance to human disturbances, I hypothesis that breeding success will be lower at nest sites located closer to increased human presence (hypothesis 5).

1.7 Dissertation structure

This dissertation comprises four chapters. The first chapter introduces cranes and the factors affecting their decline. The literature review extends this focus but shifts towards this study's focal species, the GCC. I focus on this species' breeding and the challenges of monitoring wetland nesting birds and end the review by discussing traditional and novel monitoring methods to identify an improved monitoring method for the focal species' breeding. I also outline this dissertation's aims and research questions in this chapter. Chapters 2 and 3 follow the formatting of a formal scientific publication. Chapter 2 focuses on the first aim and explores the behavioural responses of GCCs to drone monitoring. Based on these responses several recommended guidelines are presented here for using drones to monitor GCCs. The third chapter addresses the second and third aims and provides insights into the breeding success of GCCs in the southern Drakensberg, KwaZulu-Natal. I also outline the macro-environmental factors associated with this species' breeding success. The fourth chapter outlines the study's key findings in relation to its research aims and research questions, the implications of these findings and areas of focus for future studies and research.

1.8 Ethics statement

This study was performed under the ethics clearance obtained from the University of South Africa's Animal Research Ethics Committee (2022/CAES_AREC/173), and experiments were permitted under a permit granted by Ezemvelo KZN Wildlife (permit no. OP 3311/2022). All drone flights were conducted following the regulations of the South African Civil Aviation Authority.

Chapter 2: Drones as a tool to study and monitor endangered Grey Crowned Cranes (*Balearica regulorum*): behavioural responses and recommended guidelines

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Dedication

I dedicate this chapter to Pete Clowes and Julie Braby, without whom this chapter would not have been initiated. The following quote can describe your selfless contributions:

> *"The true meaning of life is to plant trees, under whose shade*
> *you do not expect to sit." - Nelson Henderson*

2.1 Title

Drones as a tool to study and monitor endangered Grey Crowned Cranes (*Balearica regulorum*): behavioural responses and recommended guidelines.

2.2 Abstract

Crane populations are declining worldwide, with anthropogenically exacerbated habitat loss emerging as the primary causal threat. The endangered Grey Crowned Crane (*Balearica regulorum*) is the least studied of the three crane species that reside in southern Africa. This data paucity hinders essential conservation planning and is primarily because of ineffective monitoring methods and this species' use of inaccessible habitats. In this study, I compared the behavioural responses of different Grey Crowned Crane social groupings to traditional on-foot monitoring methods and the pioneering use of drones. Grey Crowned Cranes demonstrated a lower tolerance for on-foot monitoring approaches when compared with drone flights. They also allowed closer monitoring approaches with drones (22.72 (95 % confidence intervals – 13.75, 37.52) m) than on-foot (97.59 (86.13, 110.59) m) before displaying evasive behaviours. The behavioural response of flocks was minimal at flight heights above 50 m, whilst larger flocks were more likely to display evasive behaviours in response to monitoring by either method. Families displayed the least evasive behaviours to lower flights, whereas nesting birds were sensitive to the angles of drone approaches. These findings confirm the usefulness of drones for monitoring wetland-nesting species and provide valuable species-specific guidelines for monitoring Grey Crowned Cranes. However, future studies on wetland breeding birds are encouraged to develop species-specific protocols before implementing drone methodologies.

Keywords: breeding; disturbance effects; drones; on-foot monitoring; protocol.

2.3 Introduction

Wetlands are among the most efficient and diverse ecosystems globally (Balwan & Kour, 2021). They play a crucial role in controlling climate change, sustaining the global hydrological cycle, conserving biodiversity, and improving human well-being (Mitsch et al., 2015; Kingsford et al., 2016; Xu et al., 2019; Nováková & Robovský, 2021). Despite their importance, almost 50 % of wetlands have been lost globally, thereby negatively affecting biodiversity and ecosystem functioning (Xu et al., 2019). Effectively implementing monitoring programmes is essential for safeguarding the remaining wetland ecosystems and their distinct contributions (Bal et al., 2018; Lindenmayer & Likens, 2011; Malhi et al., 2020; Williams et al., 2021). Birds often play a key role in these efforts, serving as reliable ecological indicators because of their well-established research history, widespread distribution across various habitats, and predictable responses to environmental changes (Fraixedas et al., 2020).

Cranes belong to the *Gruidae* bird family and commonly act as ambassadors of natural ecosystems. However, following significant declines in their populations, eleven of the fifteen crane species are classified as threatened, placing them among the most endangered bird families in the world (Harris & Mirande, 2013; Krajewski et al., 2010). Their decline is primarily attributed to habitat loss (Harris & Mirande, 2013; Austin et al., 2018; Amulike et al., 2020) with numerous species struggling to obtain successful breeding outcomes as a result of breeding site loss or degradation (e.g., Su & Zou, 2012; Fakarayi et al., 2016). Yet other crane species have shown greater resilience and a noticeable population growth following increased foraging opportunities in agricultural landscapes (e.g., van Velden et al., 2017; Fox et al., 2019; Hemminger et al., 2022). While the revival of these populations can be seen as a success, an increased dependence of cranes on croplands has also led to a conflict between farmers and cranes, presenting its own set of challenges (Lacy et al., 2015; Austin et al., 2018; Hemminger et al., 2022). This poses a particular concern for South Africa's endemic, small-ranging Blue Crane, and the Grey Crowned Crane (*Balearica regulorum*, hereafter GCC), sub-Saharan Africa's most endangered crane species (Beilfuss et al., 2007; Harris & Mirande, 2013).

Despite its precarious status, the GCC, like other crane species, exhibits significant potential as an indicator species for wetland-grassland ecosystems (Kanyamibwa, 1993; Han et al., 2017; Austin et al., 2018; Fraixedas et al., 2020) and will be the focal species of this study. Grey Crowned Cranes generally aggregate in three kinds of groupings: pairs prior to nesting, families after hatching, and flocks after fledging (Wamiti et al., 2020). Monitoring this species, especially during their breeding period (when gathered as pairs or families), is challenging as they prefer to nest in dense, inaccessible vegetation among tall reeds in wetlands and inland waterbodies (Harris & Mirande, 2013; Fakarayi et al., 2016; Olupot, 2016; Wamiti et al., 2020; Wen et al., 2021; Francis et al., 2022). The most common method for collecting breeding metrics at crane nest sites is by utilising lengthy, physical on-foot observations to identify breeding cues followed by wading to nest sites (Wamiti et al., 2020; Wen et al., 2021). This method can be unreliable and invasive (Zelelew et al., 2019), potentially disturbing breeding activities through nest abandonment and creating direct pathways to the nest sites for natural predators (Coverdale, 2006; Champagnon et al., 2019; Wamiti et al., 2020; Francis et al., 2022; Wamiti et al., 2022). The nesting preference of GCCs and ineffective monitoring methods have resulted in major knowledge gaps in GCC ecology and reproductive success, hindering the development of effective conservation strategies.

Piloted aeroplane surveys are beneficial when covering large areas over short periods, which minimises the chance of repeatedly detecting individual birds or flocks and improving population estimates (Kingsford & Porter, 2009; Galloway-Griesel et al., 2022). However, apart from being a major cause of research-related mortalities (Sasse, 2003), aerial surveys are generally suited to larger-sized animals, open habitats, and clear weather and often require specific flight paths (Hedges & O’Brien, 2012; Marchowski et al., 2018). Financially, aerial surveys can be more costly (Anderson & Gaston, 2013) but could be more cost-effective if on-foot observers require payment or if the area to be monitored is difficult to access (Marchowski et al., 2018). Because of these limitations, aeroplane-based monitoring of cranes in KwaZulu-Natal are only conducted once a year during winter, primarily focusing on monitoring the previously declining Wattled Crane (*Bugeranus carunculatus*) breeding populations (Galloway-Griesel et al., 2022). Although this method has effectively monitored GCC population trends (as GCCs flock during winter), it does not allow for effective monitoring of this species’ breeding, which takes place during the summer months.

Drones have often been demonstrated to be a more versatile and cost-effective alternative to traditional monitoring methods (Hodgson et al., 2016; Sorrell et al., 2023). Numerous studies have reported using drones to obtain precise counts and accurate identification of breeding populations of multiple bird species (Afán et al., 2018; Hodgson et al., 2018; Lyons et al., 2018; Marchowski et al., 2018; Wen et al., 2021). Using drones to monitor breeding outcomes can also reduce the time spent around nest sites (Sikora & Marchowski, 2023). Despite their usefulness, drones can cause disturbance to animals (Mulero-Pázmány et al., 2017; Schroeder et al., 2020; Duporge et al., 2021; Schad & Fischer, 2022), with birds being, on average, more sensitive to drone monitoring than other vertebrate types (Mulero-Pázmány et al., 2017; Rebolo-Ifrán et al., 2019). Guidelines for using drones to study animals usually suggest that small drone sizes (< 2 kg), implementing further take-off distances from animals, higher flight heights, slow speeds and horizontal rather than vertical approaches can reduce the disturbance imposed on birds, but these responses can vary between species (Vas et al., 2015; Lyons et al., 2018; Weimerskirch et al., 2018; Barr et al., 2020; Duporge et al., 2021; Marchowski, 2021; Wilson et al., 2021; Sorrell et al., 2023). Drone use in crane research and monitoring is in its infancy, with studies generally using drones to estimate population densities (e.g., Sandhill Cranes *Grus canadensis* (Stark et al., 2017), Siberian Cranes *Leucogeranus leucogeranus* (Wen et al., 2021) and Common Cranes (*Grus grus*) (Chen et al., 2023)). Exploratory work investigating 33 bird species has shown that drones generally impart minimal disturbance when counting populations; however, the responses of Common Cranes in this study were inconclusive (Marchowski, 2021). As such, a formal investigation into whether drones can effectively monitor cranes and, if so, how they should be flown needs to be undertaken.

This study compared the behavioural responses of three GCC social groupings (pairs, families, and flocks) to two monitoring methods: on-foot approaches at varying distances by a human observer and different drone flight heights. It also evaluated the responses of breeding birds (pairs and families) to two distinct approach angles (diagonal versus vertical). I predicted that closer on-foot distances, lower drone flight heights, and vertical drone approach angles would increase disturbances to crane groupings. Finally, this study determined the distances at which the probability of GCC groupings displaying evasive behaviours (e.g., walking or flying away) exceeded the probability of no evasive behaviour. These findings collectively contributed to developing appropriate monitoring guidelines for GCCs and other large bird species residing in difficult-to-access environments.

2.4 Materials and methods

2.4.1 Study area

This study took place in the southern parts of KwaZulu-Natal, South Africa, primarily around the Underberg, Franklin, and Kokstad regions. This summer-rainfall region (650 to 1000 mm per annum) has large areas of open grasslands and wetlands. Agriculture (intensive cropping and dairying, extensive beef, and sheep) and commercial forestry (*Pinus spp.* and *Eucalyptus spp.*) are the primary land-use types in these regions.

2.4.2 Experimental design

Experiment 1: Monitoring method comparison experiment

Although physiological measurements provide the ultimate indication of stress in animals and should be encouraged where possible (Weimerskirch et al., 2018; Geldart et al., 2022; Zink et al., 2023), changes in animal behaviour are often immediate (Borrelle & Fletcher, 2017) and can provide cost-effective metrics of animal stress. Trial observations included recording the behavioural cues of GCC groupings (pairs, families, and flocks) in response to either of the two monitoring methods (on-foot, drone) across various distances and flight heights. Behavioural cues were categorised similarly to those outlined in Vas et al. (2015) and Cantu De Leija et al. (2023) and with personal observations of GCC behaviours. These categories were as follows: no behaviour change (1), heads raised to observe surroundings (2), wings raised (3), moving away (4), and flying away (5) (Figure 2.1). All trial observations were undertaken by the same observer (CRD), and care was taken to wear similarly coloured clothing for each of the trials to control for the impact that certain clothing colours can have on bird flight initiation distances in rural areas (Zhou & Liang, 2020). Most observations took place on days when weather was suitable for drone flights (clear and warmer days), while early mornings and late afternoons were generally avoided as shadows from surrounding vegetation obstructed visuals of nesting activities during these periods (Demmer pers. obs.).

On-foot monitoring

Upon locating a GCC grouping, the observer approached the group at a normal walking speed of approximately 1 m.s^{-1} (e.g., Mikula et al., 2023), making a reasonable effort not to disturb the grouping (e.g., avoiding noises and sudden movements).

Observations were noted at the start of each trial, every 10 – 15th step thereafter, and again if any change in GCC behaviour was observed. Each observation included measuring the distance between the observer and the grouping using a range finder (Vortex Crossfire HD LRF-CF1400 Rangefinder) and taking a photograph (Nikon D7200 with 100-400 mm Sigma lens) of the group, which enabled *post-hoc* behaviour coding. Observations were recorded until groupings displayed a type 5 response (flying away) (Figure 2.1).

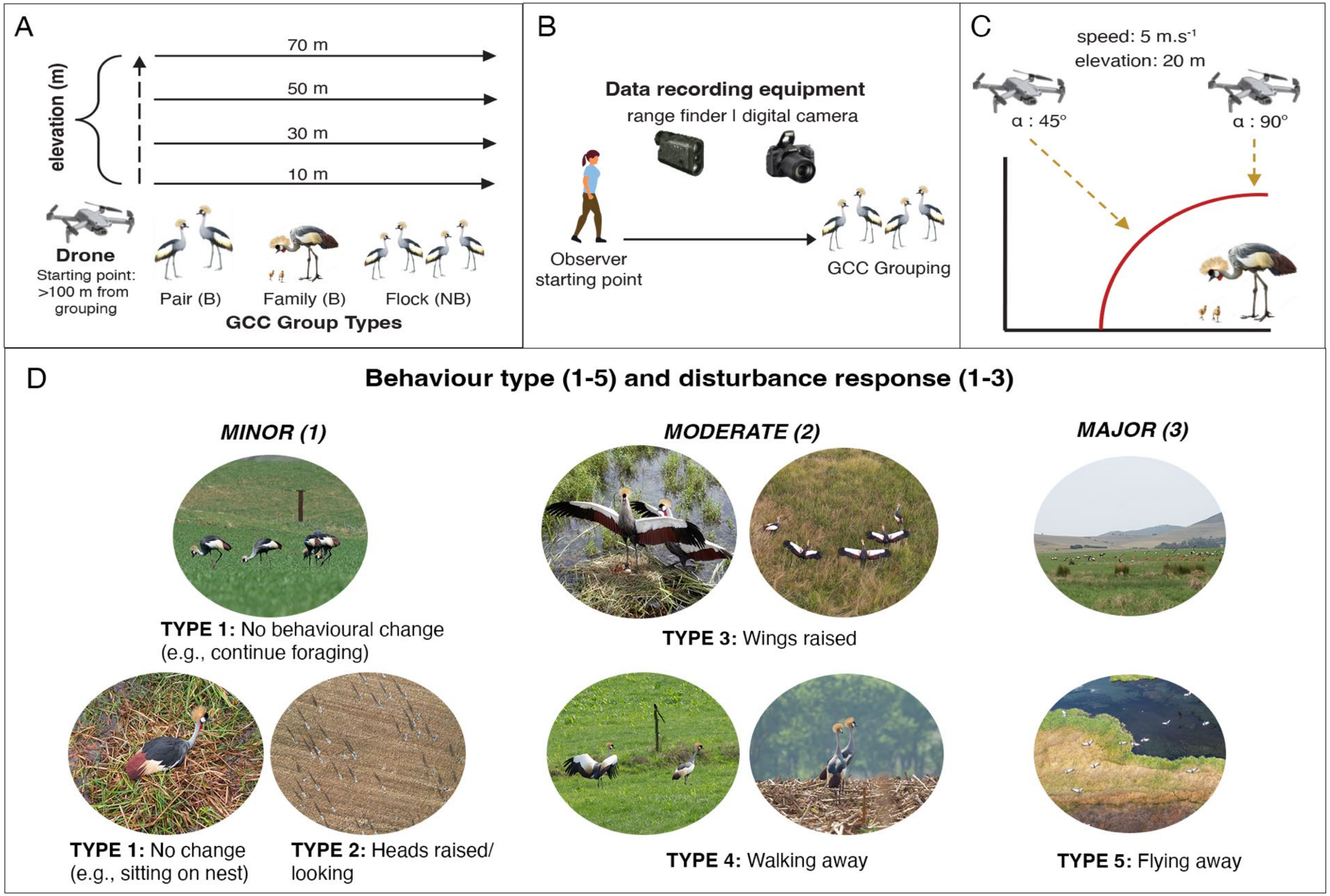

Figure 2.1: Visual depiction of (a) schematic representation of systematic drone flight paths to test bird response to the presence of a traversing drone, B = breeding and NB = non-breeding social groupings; (b) on-foot methodology, using a range finder to determine distance between observer and subject grouping and a digital camera to capture the behavioural responses of subject groupings as the observer approaches, (c) schematic representation of the breeding bird approach experiment and (d) behaviour response types as seen from drone and on-foot approaches. Behaviour types 1–5 are representative of the behaviour response types used for the majority of analyses. Disturbance responses 1–3 are representative of the responses used for the approach angle investigation.

Drone methodology

The drone pilot was positioned at least 100 m from GCC groupings before drone take-off, as per Vas et al. (2015), and at a similar elevation to the GCC grouping. On some occasions, the pilot found it practically impossible to position herself at 100 m from the grouping. When this was the case, the drone was deployed from at least 80 m from the GCC groupings. The drone was deployed from the pilot's location to a randomly pre-selected flight height (10, 30, 50, or 70 m above the deploy point), then flown over the grouping at the selected flight height at a speed approximating 5 $m.s^{-1}$ with video recording activated to facilitate *post-hoc* behaviour coding (Figure 2.2). After reaching the grouping, the drone was flown approximately 80 m beyond the grouping and then returned to the deployment point to avoid flying over the grouping during the return flight. All drone flights were conducted using a standard Mavic Air 2S drone (DJI Technology Co., Shenzhen, China) (595 g, 1-inch 20 MP sensor, 8× zoom, 65 dB low noise propeller).

It was challenging to determine the precise height of the drone above the grouping *in situ* as the drone only reports flight height relative to the take-off point. The flight heights above GCC groupings were therefore determined *post-hoc* by extracting elevation values for the drone deployment and subject locations from a high-resolution (± 2 m) digital elevation model (GeoSmart Space, 2019) of the study area using the coordinates as recorded by the drone's Global Positioning System. The drone's actual height was therefore calculated as:

$$flight\ height = elevation_{deploy} + height_{UAV} - elevation_{group}$$

where flight height is the actual height of the drone above the grouping, $elevation_{deploy}$ is the elevation above sea level of the point from which the drone was deployed, $height_{drone}$ is the flight height reported by the drone flight log for the point at which the drone was above the grouping and $elevation_{group}$ is the elevation above sea level for the point where the grouping was located.

Figure 2.2: Example footage captured during monitoring observations. Individual birds were numbered with different colours to differentiate between behavioural responses.

Data collection from each grouping continued until a maximum of four trials had been recorded (with a 10-minute interval between trials to allow birds to return to their prior behaviour) or until the subjects flew beyond the range of the drone. As a precaution, the drone was always flown manually to allow the pilot to easily manoeuvre and control the drone to avoid any potentially aggressive behaviour from the target or non-target species in the study area. Each site was scanned for non-target species using binoculars before beginning a drone mission. Whilst in flight, the pilot remained aware of any new individuals of the target or non-target species entering the site. As far as practically possible, flights over any non-target species were avoided. If any non-target species displayed behavioural signs of discomfort in the drone's presence (e.g., aggressive behaviour towards the drone from territorial or breeding birds or birds of prey, obvious fleeing from the environment after launching the drone demonstrating substantial fear, evidence of nesting or breeding by non-target species) the pilot avoided flying whilst that species was near the flight route; if territorial, future flights at that site were terminated.

Post-hoc behavioural coding

Each photograph taken during the on-foot monitoring experiment was considered an observation. From each video recorded during the drone monitoring experiment, the frame directly above the grouping was extracted and used as the observation. If birds responded with a type 5 response before the drone reached the grouping, the frame closest in time was used to determine the drone's position whilst focusing on the initiated flight response of the grouping. Individual birds' behaviour (type 1 – 5) was identified and noted at each observation, and the total number of subjects displaying each of the five behaviours was recorded.

Experiment 2: Nesting approach experiment

Breeding behavioural cues consisted primarily of a lone crane foraging near a water body or wetland (Wamiti et al., 2020). Breeding birds were observed both during nesting (parents and chicks situated at the nest) and after nesting (parents and chicks observed away from the nest, either in reeds or foraging along the shoreline or in croplands, grasslands or pastures). Once identified, I used a drone to locate the potential nest site or the breeding birds. If either of these were found, I recorded it as an observation. At approximately 20 m from the subject, the drone was lowered to a flight height of approximately 20 m. The drone was then manoeuvred towards the subjects either by flying diagonally (an angle of approximately 45°) or vertically (flying horizontally until above the subjects and then descending at an angle of approximately 90°), slowly descending until approximately 7.5 m from the subjects. The distances reported here are approximate because of the limitations of determining distances *in situ* via the drone. Video recording was enabled throughout the approach to facilitate *post-hoc* behavioural coding as follows: (1) little disturbance (either looking, remaining sitting, holding ground, or standing up), (2) moderate disturbance (raising wings, walking, or running away from offspring), or (3) major disturbance (flying away from offspring). A schematic representation of this method is provided in Figure 2.1C.

2.4.3 Statistical analyses

Individual images represented ordinal trials, and coded behavioural responses served as the independent variable. The number of birds displaying each response was then determined for each image.

Three analyses were conducted to assess the impact of either monitoring method on the behaviour of GCCs. I evaluated i) the average distance at which a particular behavioural response was observed when monitoring non-nesting GCCs on foot (monitoring method comparison experiment), ii) the effect of drone flight height on the behavioural scores of non-nesting GCC group types (drone flight height experiment) and iii) the effect of approach angle on the behavioural response of nesting GCCs (nesting approach angle experiment). All analyses were conducted using R 4.2.2 (R Core Team, 2022), and *post-hoc* comparisons were generated using the *emmeans* R package (Lenth, 2023) with *p*-values adjusted using the Tukey method for multiple comparisons. Averages are presented as means (± 95 % confidence intervals) both in-text and in figures. Significance was determined at $p < 0.05$.

Experiment 1: Monitoring method comparison experiment

The distance at which the categorised GCC behaviours were observed between the two methods was modelled using a linear mixed effect regression (Equation 1) using the "lmer" function from the *lme4* R package (Bates et al., 2015). Behavioural response (categorical with five levels), monitoring method (categorical with two levels – "On-foot", "Drone") and their interaction were included as fixed effects. Subject grouping ID was included as a random effect to control for repeated measurements on distinct subject groupings (random effect $LRX^2 = 24.35$, df = 1, $p < 0.001$). Controlling for subject grouping also assisted in controlling for variation in start distance during the on-foot monitoring approach. The model was weighted by the proportion of birds within the observation exhibiting the behaviour type at each distance, and the distance was log-transformed to improve the normality of the residuals (Zuur & Ieno, 2016).

$$Distance_{ij} \sim N\left(\mu_{ij}\right)$$

$$E\left(Distance_{ij}\right) = \mu_{ij}$$

$$\log\left(\mu_{ij}\right) = Behaviour_{ij} + Method_{ij} + Behaviour_{ij} \times Method_{ij}$$

$$SubjectID_i \sim N(0, \sigma^2)$$

(Equation 1)

where $Distance_{ij}$ is the jth observation of $SubjectID\ i$, and $SubjectID_i$ is the random intercept with is assumed to be normally distributed with a variance of σ^2.

The second analysis considered the type of behavioural responses exhibited across group types and the distance between the observer and the subject grouping when being monitored on-foot (Equation 2). I used a cumulative link mixed effects model (clmm) with a logit link function (implemented using the *ordinal* R package, (Christensen, 2022) to model the behaviour response (an ordinal, non-normally distributed measurement). Cumulative link models are used to handle ordinal, non-continuous response data with the output determining the probability of each level of the response occurring. Group type (a factor with three levels; “Pair”, “Family”, “Flock”), distance to the subject grouping (covariate) and the interaction of these two variables were included as fixed effects. Although the inclusion of subject grouping ID as a random effect to control for both repeated measurements and differences in monitoring start distance did not significantly improve the model (LRX^2 = 0.418, df = 1, p = 0.518), it was included as the results were more conservative under the model with the random effect structure compared with the model without this structure.

$$P\left(Behaviour_{ijk} \leq k\right) \sim multinom\left(\mu_{ijk}, 1\right) \, for \; k = 1, 2, \ldots, 5$$

$$E\left(Behaviour_{ijk}\right) = \mu_{ijk}$$

$$\text{logit}\left(Behaviour_{ijk}\right) = \beta 0_k - \left(GroupType_{ij} + Distance_{ij} + GroupType_{ij} \times Distance_{ij}\right)$$

$$SubjectID_i \sim N(0, \sigma^2)$$

(Equation 2)

where $Behaviour_{ijk}$ is the jth observation of the kth behaviour response type of $SubjectID\ i$, $\beta 0_k$ is the threshold parameter for behaviour response type k and

$SubjectID_i$ is the random intercept with is assumed to be normally distributed with a variance of σ^2.

A cumulative link model (clm) was used to model the behavioural responses to drone monitoring using a similar approach to that described in Equation 2 (but without the random effect structure) in the *ordinal* R package. The effect of individual subjects was considered minimal because of i) the extended nature of these observations, ii) the random ordering of heights flown, and iii) the movement of individuals between groupings and between trials, and it was therefore not recorded or incorporated into this analysis. Behaviour responses did not vary significantly because of drone deployment distance ($\chi^2 = 1.429$, df = 1, $p = 0.232$), so its effect was not incorporated into the model. Drone height above the GCC grouping (covariate) and the group type being observed (a factor with three levels – “Pair”, “Family”, and “Flock”), together with the interaction of these two variables, were included as fixed effects. I determined the distance at which the most evasive behaviours (moving and flying away) would occur more than 50 % of the time for both monitoring methods. This indicated the grouping’s flight initiation distance – a standard metric used to compare stress induced through bird monitoring methods (Blumstein, 2006).

A separate clm was used to assess the behavioural response of flocks to the number of birds in the flock (covariate) and the distance to the flock (covariate) for each monitoring method (Equation 3). Because of the smaller sample size used for on-foot monitoring, the clmm did not converge, so the effect of flock ID was ignored. The interactions of these two fixed effects were non-significant in both models and were therefore excluded from the final models. Test statistics for clm models are presented as X^2 values and as likelihood ratio X^2 (LRX^2) values for clmm models.

$$P(Behaviour_{jk} \leq k) \sim multinom(\mu_{ijk}, 1)\ for\ k = 1, 2, \dots, 5$$

$$E(Behaviour_{jk}) = \mu_{jk}$$

$$\text{logit}(Behaviour_{jk}) = \beta 0_k - (FlockSize_j + Distance_j)$$

(Equation 3)

where $Behaviour_{jk}$ is the jth observation of the kth behaviour response type and $\beta 0_k$ is the threshold parameter for behaviour response type k.

Experiment 2: Nesting approach experiment

This experiment assessed the level of disturbance experienced by breeding GCCs at diagonal or vertical approach angles. Disturbance level was an ordinal, non-normally distributed response variable, and data collection included reoccurring observations made on the same GCC breeding subjects at specific nest sites. To account for this, I modelled the disturbance level using a clmm from the ordinal R package (Equation 4). Approach angle (a factor with two levels – "Vertical", "Diagonal") and reproductive stage (a factor with two levels - "During nesting", "After nesting") were included as fixed effects together with their interaction. Breeding pair ID was incorporated as a random effect to control for reoccurring observations on the same breeding subjects (LRX^2 = 5.435, df = 1, p = 0.0197).

$$P(Disturbance_{ijk} \leq k) \sim multinom(\mu_{ijk}, 1)\; for\; k = 1, 2, 3$$

$$E(Disturbance_{ijk}) = \mu_{ijk}$$

$$\begin{aligned}\mathrm{logit}(Disturbance_{ijk}) \\ = \beta 0_k - (Angle_{ij} + ReproductiveStage_{ij} + Angle_{ij} \times ReproductiveStage_{ij})\end{aligned}$$

$$BreedingPairID_i \sim N(0, \sigma^2)$$

(Equation 4)

where $Disturbance_{ijk}$ is the jth observation of the kth behaviour response type of $BreedingPairID\ i$, $\beta 0_k$ is the threshold parameter for behaviour response type k and $BreedingPairID_i$ is the random intercept with is assumed to be normally distributed with a variance of σ^2.

2.5 Results

In total, 313 drone flights were conducted: 110 over pairs, 66 over families, and 110 over flocks. The flight time totalled 2108 min and approximated 6 min and 44 sec per flight. Of 56 on-foot approaches, 26 were to pairs, seven to families, and 23 to flocks. The mean number of birds (± 95 % confidence intervals) in each grouping was 2 (2, 2) for pairs, 3.66 (3.20, 4.13) for families, and 34.4 (34.04, 36.08) for flocks.

2.5.1 Monitoring methodology study

Regardless of the method used, individual birds within a grouping displayed distinct differences in their behaviour type depending on the distance of the observer or drone from the bird grouping ($F_{4, 789.77}$ = 23.704, p < 0.001; Figure 2.3A). Birds showed no response at the furthest distances. As the observer moved closer to the bird, it was more likely that the bird would look, move away, and finally fly (Figure 2.3A). Wings

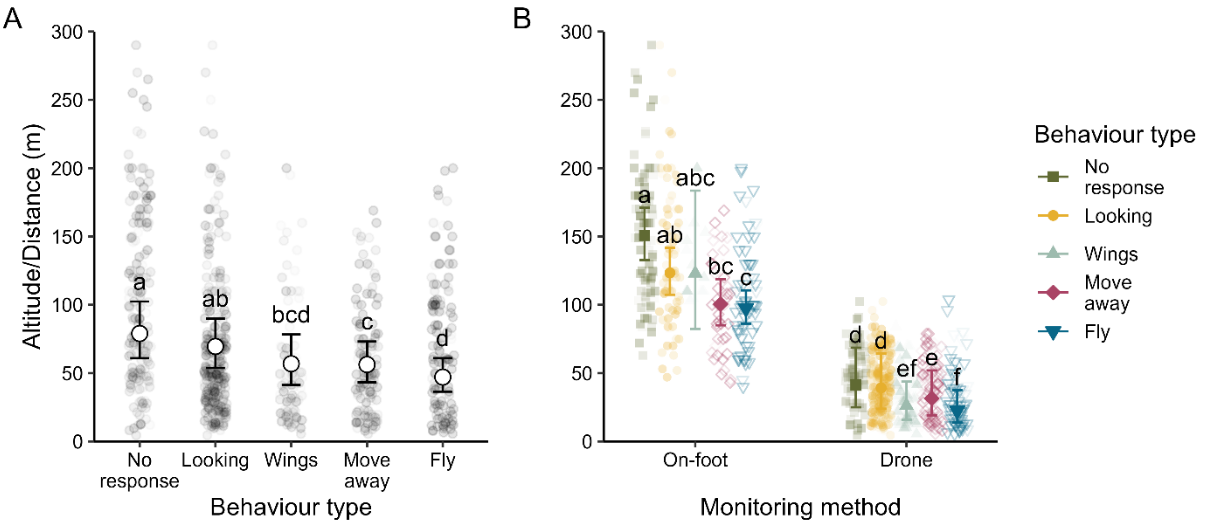

Figure 2.3: A – Mean (± 95 % confidence intervals - CI) distance (m) at which Grey Crowned Cranes (GCC) exhibited behaviour responses using both monitoring methods. B – Mean (± 95 % CI) distance (m) at which GCC monitoring methods observed different behavioural response types. Responses within each panel with the same letters indicate that no evidence was found for significant differences between their means.

raised was significantly more likely to occur at closer distances than no response but often co-occurred with looking, moving away, or flying (Figure 2.3A). When the two monitoring methods are compared, the average on-foot observation was recorded at 117.52 (104.89, 131.66) m from birds being observed, and the average of all drone flight recordings was 31.39 (19.16, 51.43) m from observed birds ($F_{1,\ 17.27} = 29.572$, $p < 0.001$, Figure 2.3B). Flight responses were initiated at 97.59 (86.13, 110.59) m when monitored on-foot and at 22.72 (13.75, 37.52) m when monitored by drone. A interaction effect indicated that the change in behaviour responses across monitoring distance was not consistent across monitoring methods ($F_{4,\ 789.77} = 2.858$, $p = 0.023$, Figure 2.3B). The distances at which behavioural responses were recorded were more similar when recorded with a drone than on-foot. This was primarily because of the substantial overlap in wings being raised when birds were approached on-foot whereas raised wings was delayed and occurred at similar distances to moving away when a drone was used. On-foot monitoring induced more evasive responses as the distance between the observer and the grouping decreased ($LR\chi^2 = 41.511$, df = 1, $p < 0.001$). Evasive responses (moving or flying away) had a 50 % chance of occurring at 109 m when using on-foot monitoring. The type of social grouping did not affect the rate at which a particular behaviour response was observed ($LR\chi^2 = 2.431$, df = 2, $p = 0.297$). However, the type of behavioural response changed depending on the distance from the observer between group types ($LR\chi^2 = 7.691$, df = 2, $p = 0.021$; Figure 2.4).

Families displayed no change in their behavioural responses across all distances (Z-ratio = 0.825, p = 0.410), whilst both pairs (Z-ratio = 3.715, p < 0.001) and flocks (Z-ratio = 4.014, p < 0.001) displayed more evasive responses as the distance between the observer and the subjects (cranes) decreased. The point at which evasive responses had more than a 50 % chance of occurring was at 107 m for pairs, 52 m for families, and 123 m for flocks (Figure 2.4). significant interaction effect between the

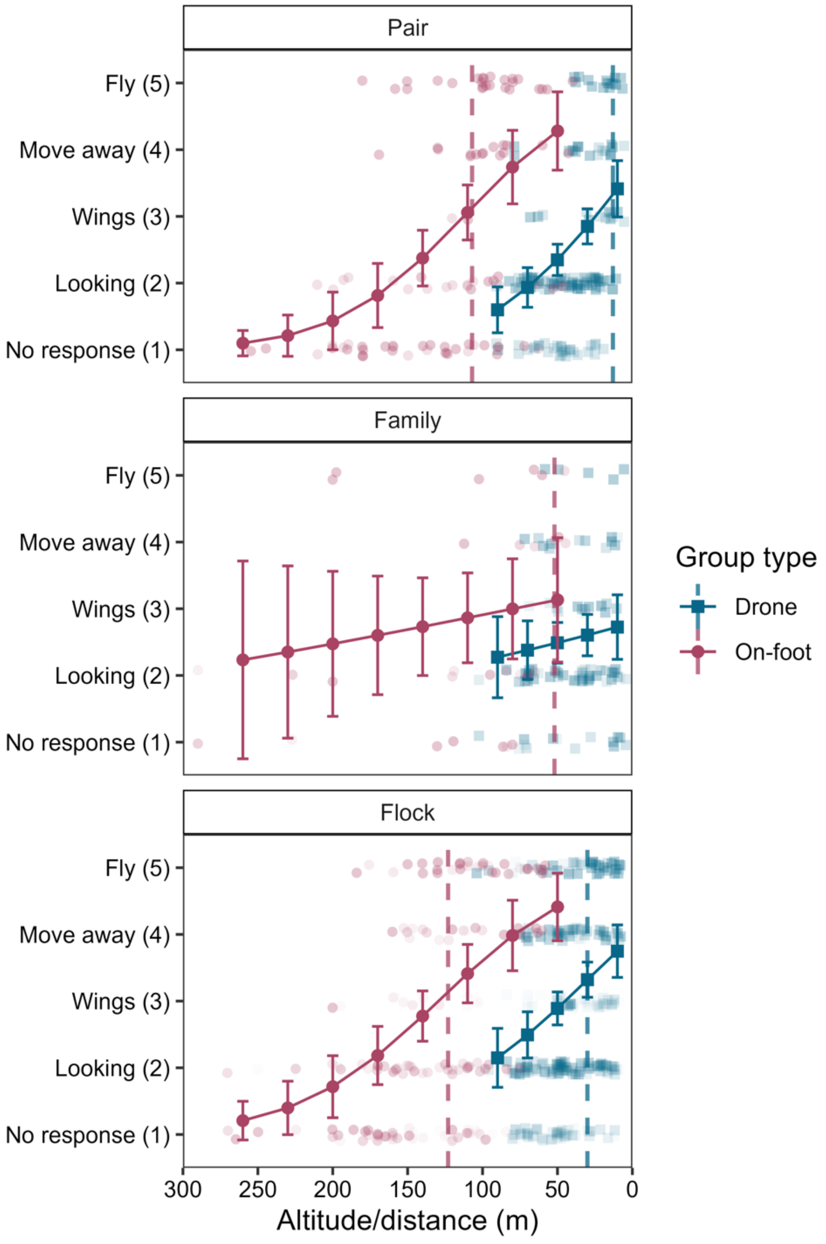

Figure 2.4: Mean (± 95 % confidence intervals) Grey Crowned Crane (GCC) behavioural response class observed across decreasing on-foot approach distance and drone flight altitude for three GCC grouping types. Dashed vertical lines indicate the flight height at which the evasive behaviours (moving or flying away) become more likely to occur than non-evasive behaviours. Drone and on-foot results were obtained from two separate analyses because of methodological differences and so are not directly comparable.

monitoring method and behaviour type.

Drone flight height study

As drone flight height decreased, GCC groupings were more likely to display evasive behaviours (χ^2 = 177.304, df = 2, p < 0.01; Figure 2.5A). Considering the changes in GCC behaviours, the probability of no response and looking decreased as drone height decreased, while the likelihood of cranes moving or flying away increased (Figure 2.5B). There was little change in the response of raising wings. The point at which evasive behaviours (moving and flying away) became more likely to occur than all other behaviour types was at 9 m.

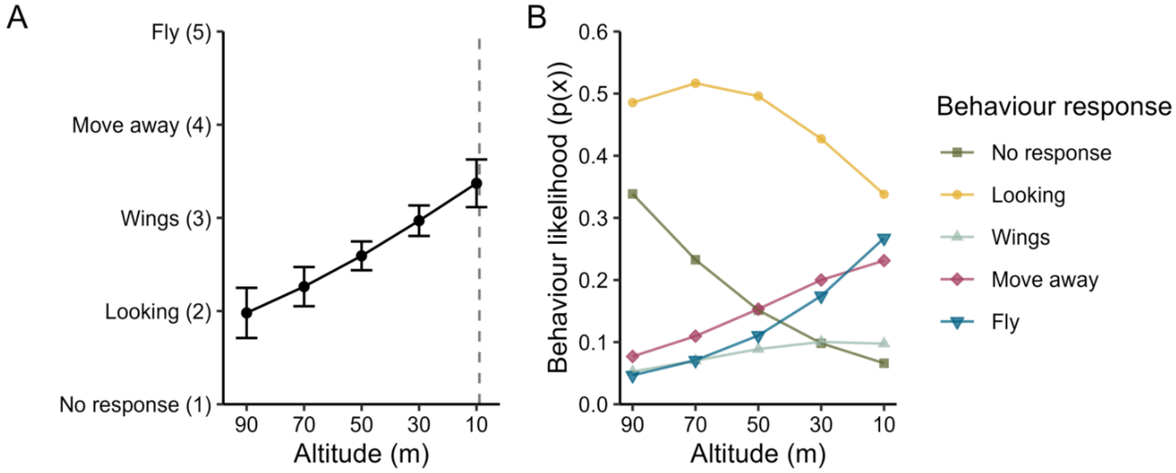

Figure 2.5: Bird responses to drone flight height. A – Mean (± 95 % confidence intervals) behaviour response class observed across decreasing drone flight altitude. Dashed vertical line indicates the point at which evasive behaviours (moving and flying away) become more likely to occur than non-evasive behaviours. B – Mean probability of a particular behavioural response being exhibited across decreasing drone flight altitude (error bars excluded for clarity).

Group types responded differently regardless of the drone's flight height (χ^2 = 34.142, df = 2, p < 0.001). Pairs and families did not differ in the type of behavioural response, with the mean behaviour class observed being between looking and raising wings (mean score = 2.55 and 2.54, respectively; Z-ratio = 0.063, p = 0.998). However, flocks generally displayed raised wings (mean score = 3.07) and were significantly more likely to evade the drone than were pairs (Z-ratio = 3.162, p = 0.005) or families (Z-ratio = 2.861, p = 0.012).

Grey Crowned Crane group types responded differently to variations in drone flight heights ($\chi 2$ = 95.175, df = 2, p < 0.001, Figure 2.4). Families showed no change in their behavioural responses across all flight heights (Z-ratio = 0.923, p = 0.356), whilst both pairs (Z-ratio = 4.571, $p < 0.001$) and flocks (Z-ratio = 3.720, $p < 0.001$) showed more evasive responses as the drone flight height decreased. Pairs displayed evasive behaviour at 13 m, whilst flocks displayed evasive behaviour at 30 m. Evasive responses were consistently less likely to occur than non-evasive responses for families across the range of drone flight heights used in this study.

There were significant changes in behaviour associated with distance to the flock and the number of birds in the flock across both monitoring methods. Reduced distance to flocks (on-foot: $\chi^2 = 23.572$, df = 1, $p < 0.001$; drone: $\chi^2 = 12.526$, df = 1, $p < 0.001$, Figure 2.6) and increased flock size (on-foot: $\chi^2 = 4.300$, df = 1, $p = 0.038$, drone: $\chi^2 = 5.801$, df = 1, $p = 0.016$; Figure 2.6) increased the chance of evasive behaviours across both monitoring methods.

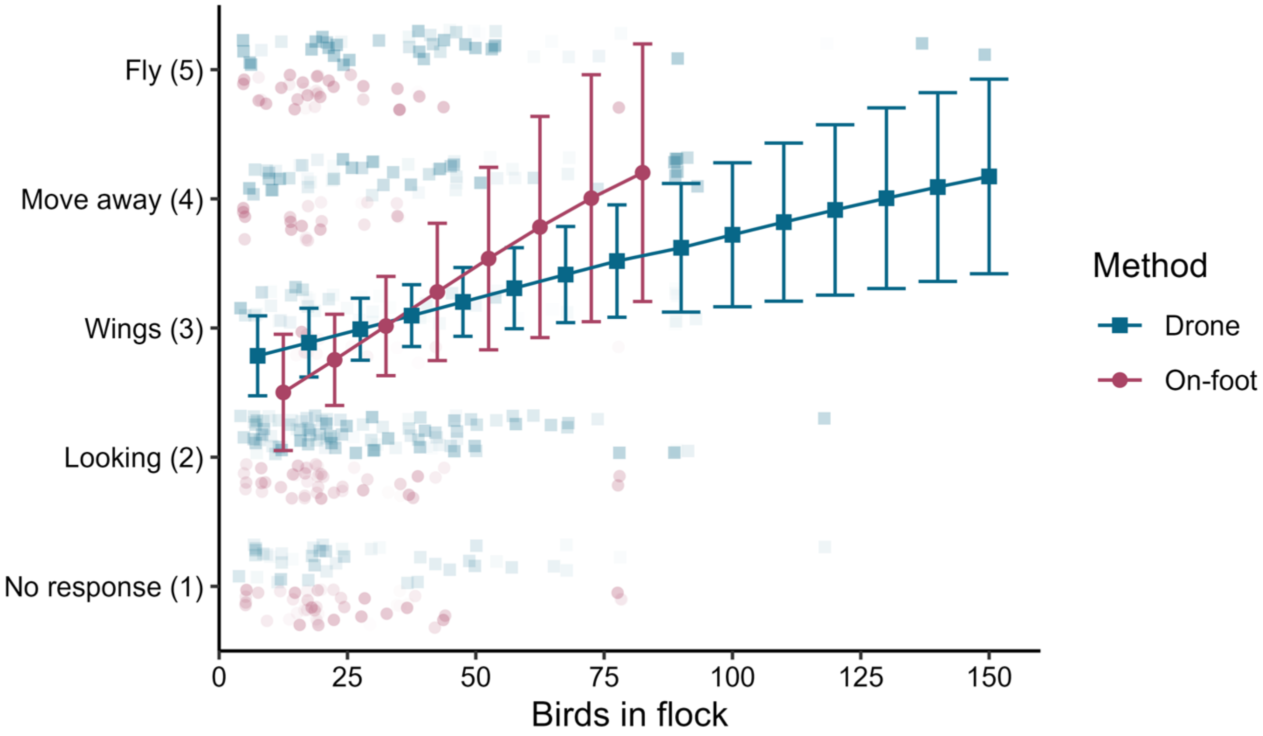

Figure 2.6: Mean (±95 % confidence intervals) behaviour response class response for Grey Crowned Cranes across flock size. The methods plotted are the result of separate statistical models. Different ranges in flock size reflect the actual range of flock sizes observed when monitoring with either method.

2.5.2 Nesting approach study

Behavioural responses of GCCs were significantly related to drone approach angles to nests or families ($LR\chi^2 = 13.989$, df = 1, $p < 0.001$, Figure 2.7), with vertical approaches causing a greater disturbance. There was also a difference in the type of responses observed between breeding stages (LRχ^2 = 9.032, df = 1, p = 0.003), with more evasive responses being observed after nesting (difference in mean class = 0.167 ± 0.07 standard errors). The interaction of these two factors (LRχ^2 = 9.032, df = 1, p = 0.003) showed that different responses to the approach angle occurred during nesting (Figure 2.7).

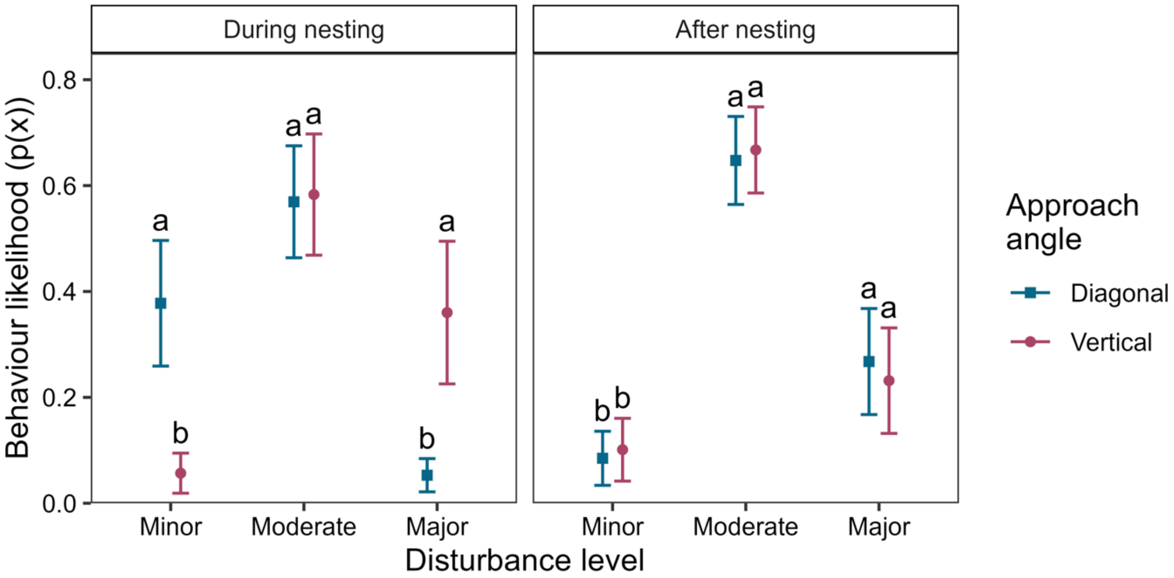

Figure 2.7: Mean probability (± 95 % confidence intervals) of perceived level of disturbance imposed on breeding Grey Crowned Cranes during and after nesting across two drone approach angles. Letters indicate the response of post-hoc analyses conducted between approach angles for each disturbance level within breeding stage. Responses within each panel with the same letters indicate that no evidence was found for significant differences between their means.

2.6 Discussion

The findings of this study confirm the usefulness of drones for monitoring wetland-nesting species and provide valuable species-specific guidelines for monitoring GCCs. By conducting a total of 313 drone flights over three GCC social groupings (pairs, families, and flocks), I found that all groups displayed disturbance cues earlier when approached on-foot than when using a drone (Figure 2.3). Flocks experienced minimal disturbance when the drone was flown above 30 meters. However, larger flocks demonstrated a higher probability of evasive responses to either of the monitoring methods. Nesting birds were sensitive to the angle at which a drone approached their nest site, but after hatching, family groupings displayed the least likelihood of evading lower flight heights. Apart from addressing important practical considerations relating to improving the monitoring of the focal species, the experiments I conducted also allowed me to explore several ethological theories, which are elaborated upon below.

2.6.1 Reaction of GCC groupings to monitoring methods

Flight initiation distance and monitoring methods

Bird body mass is positively correlated with flight initiation distance, suggesting that larger birds flee from potential threats at greater distances because they require longer take-off (Møller et al., 2016). Large-sized South African waterbirds follow this principle, displaying a flight initiation distance of approximately 100 m when approached on-foot (Coetzer & Bouwman, 2017). However, one might assume that the close association of cranes with agriculture has habituated them to human disturbances, making them less sensitive to on-foot monitoring approaches (Okes et al., 2008; Samia et al., 2015; Weston et al., 2020). Nevertheless, Black-necked Cranes (*Grus nigricollis*) flee observer approaches at 88.33 m (Kong et al., 2021), and my findings revealed that GCCs initiated flights at 97.59 m. Therefore, GCC groupings are equally tolerant of on-foot approaches as their local counterparts. These flight distances also suggest that cranes are sensitive to human disturbances (Coverdale, 2006; Végvári et al., 2011; Wang et al., 2011), yet most crane species are still monitored using on-foot methods. Monitoring GCCs with drones substantially reduced their average flight initiation distance to 22.7 m. This distance was 4.29 times closer than what on-foot monitoring could achieve. Thus, when monitoring from equal distances one can assume that drones impart less disturbance than traditional monitoring methods.

Response of flocks to monitoring methods

Flocks demonstrated evasive behaviours sooner than other social groupings, regardless of the monitoring method used. While several potential explanations could account for their alarmed response, I discuss here three of the more frequently encountered explanations. Firstly, this finding may support the vigilance hypothesis, which states that flocks with more individuals have an improved probability of detecting threats, which further escalates the likelihood of evasive flight behaviours (Morelli et al., 2019). Secondly, a flock's vigilance may depend on the type of habitat they utilise, and the number of threats associated with that habitat. Agricultural areas, for example, are known to attract opportunistic predators (Drouilly et al., 2018). Hooded Cranes (*Grus monacha*) gathering in rice paddies surrounded by human activities display higher vigilance in these areas compared with their natural habitats (Li et al., 2015). Therefore, it is perhaps not surprising to note a similar response among GCCs that gather in harvested crop fields and pastures. Samia et al. (2015) explained that birds inhabiting agricultural landscapes must learn to identify deviations from a predator or human's routine behaviour. They suggest that when such deviations occur, birds usually re-elicit a cautious or evasive response to avoid possibly lethal threats. And thirdly, GCC flocks contain numerous younger, non-breeding juveniles. These individuals may be more sensitive to anthropogenic disturbances because of inexperience. When juveniles are present, Black-necked Crane flocks increase their vigilance time, likely to compensate for a lack of experience among younger cranes (Xu et al., 2013). Flocks consisting of younger birds can also display "false alarm flighting" as practice to prepare for encountering a real threat (Root-Bernstein, 2021). Monitoring GCC flocks, which often have a higher proportion of juveniles, should thus be done with care whilst maximising the distance or flight height to reduce their flight probability.

Response of breeding birds to monitoring methods

Before employing new monitoring methods, it is essential to carefully consider any possible disturbances to a species' breeding behaviour and their environment (Coverdale, 2006; Hodgson et al., 2018; Francis et al., 2022; Wamiti et al., 2022; Cantu De Leija et al., 2023; Zink et al., 2023). The nesting phase is the most vulnerable period for many threatened ground-breeding birds (Assersohn et al., 2021). Findings indicate that half of Whooping Crane (*Grus americana*) chick mortalities occur during hatching and before the chicks are one month old (King et al., 2013), while the hatching rate of GCCs is also low (Chapter 3; Gichuki, 2000). While any approach to a nest site or family grouping for monitoring purposes likely causes some level of disturbance, researchers should note the response of the parents, which may vary depending on the perceived level of danger to either themselves or their offspring (Lima, 2009; Dowling and Bonier, 2018). For example, Piping Plover (*Charadrius melodus*) parents flee their nest at greater distances when the approaching subject is a dog in contrast to approaching humans or vehicles since the latter is likely perceived as less threatening (Jorgensen et al., 2016; Dowling and Bonier, 2018).

Nesting GCCs generally showed increased vigilance when monitoring with either method. Although drones could obtain closer distances, birds tended to flee from nest sites when approached vertically (tactics often employed by aerial predators – Vas et al., 2015) as opposed to diagonally. Days after hatching, cranes leave the security of their nest and undertake substantial movements with their young (Veltheim et al., 2019). During this period, parents were less sensitive to approach angles and were less likely to leave their chicks. When approached by either method at closer distances, GCC parents called, hopped, and raised their wings (with younger chicks hiding under their parents' wings). The behaviours allude to their instinctive priority to protect their offspring by distracting predators from their offspring or to increase their perceived size as a predation deterrent (Humphreys & Ruxton, 2020; Gallego & Sarasola, 2021), likely hoping that the potential threat might eventually stop or change direction. Their behaviour during and after nesting thus appears to align with the parental theory, which suggests a positive correlation between parental defence and offspring age (Boucher, 1977). When applied to this species, this would mean that incubating cranes likely prioritise their own safety over the success of their eggs yet appear to undergo a switch once eggs have hatched since the probability of successfully rearing young increases after hatching (similar findings shown by Ge et al., 2011 and Kong et al., 2021).

2.6.2 Species-specific guidelines and future recommendations

While drones may emit some disturbance to GCC groupings and collisions of a drone and target or non-target species are possible, the latter is rare and did not occur once during the 313 flights of this study (similar results have been obtained by Marchowski, 2021). The risk of disturbance and collisions from drones should thus be placed within the context of the risks and inefficiencies of on-foot monitoring. For example, monitoring tern nests with drones is 2.89 times faster than on-foot observations (based on information provided in Valle & Scarton, 2021). Also, if Stork (*Ciconia Ciconia*) parents leave their nests during monitoring events, their return time to the nest is shorter when monitored with drones than on-foot monitoring (Zbyryt et al., 2021), further emphasising the reduction in stress from drone monitoring. Although I did not explicitly measure return timing, informal observations suggest similar trends when monitoring GCCs with drones. In summary, the discussed findings thus far indicate clear advantages in utilising drones for GCC monitoring and guidelines for doing so will be expanded upon below. Although drones have many benefits, they do require greater postprocessing to extract data from the images or videos (Gonzalez et al., 2016). Additionally, factors like the drone's initial cost and civil aviation requirements, including drone pilot training and registration, must be considered before adopting this monitoring tool (Hodgson et al., 2016; Sorrell et al., 2023). When considering vulnerable species that are sensitive to human disturbances, the trade-off of longer postprocessing times in exchange for shorter exposure times may well be worth it.

Monitoring flocks with drones

Drones are generally used to monitor flocks for census purposes (Hodgson et al., 2018; Valle & Scarton, 2020; Marchowski, 2021; Wen et al., 2021). However, in this study, flocks responded negatively to flight heights below 30 m. Drones should then be flown at elevated flight heights to flight responses. Censuses typically require flying at greater altitudes (> 50 m) to capture more individuals in the frame, so there is little trade-off in higher flight heights. Notably, using drones as an alternative to annual aeroplane surveys would serve as a more regular and cost-effective method to obtain valuable data which can be used to inform this species' conservation strategies.

Monitoring breeding birds with drones

Drones were very effective in monitoring GCC breeding pairs and family groupings. To capture breeding activities clearly, I suggest monitoring nest sites after early mornings and before late afternoons (Demmer pers. obs.). Once a potential nest site has been located, the drone should be manoeuvred in a way that minimises the angle of approach in order to minimise the parents' escape probability. Researchers should also note that displaying no behavioural response to a disturbance stimulus does not necessarily mean that the subject is not stressed, since stress may manifest through physiological responses instead (Zink et al., 2023). As such, I discourage unnecessarily disturbing incubation and parental activities (both of which are energetically costly to the parents – Geldart et al., 2022) and suggest limiting flights during these initial breeding stages, as parents are more likely to leave the nest. The drone should therefore be flown at higher flight altitudes to record a nest's co-ordinates and the drone's digital zoom capabilities should be used to capture a photo of the nest activities when parents are not actively incubating (e.g., standing, flying off, or during incubation shifts). Although parents showed no behavioural change in response to drone approach angles after nesting, I suggest continued caution when flying at closer distances and suggest using diagonal approaches throughout all flights over pairs and families (birds may find it uncomfortable to rotate their heads to assess vertically approaching threats and crane groupings generally fled when approached from above).

Future studies should also employ regular monitoring, especially when tracking families with older chicks at wetlands (as opposed to human-constructed waterbodies) since these waterbodies often have multiple nest sites, which can lead to confusion and inaccurate data capturing. Families with older or fledged chicks travelled further

(Wolfson et al., 2020; Thompson et al., 2022; Wamiti et al., 2022) and were sometimes more easily located by surveying the area with a vehicle instead of a drone. In some scenarios, attaching GPS bands has proven useful in monitoring Brolga Crane chicks (*Antigone rubicunda*) with minimal fatalities (Veltheim et al., 2019), but this was not the focus of my study.

2.6.3 Conclusions

This study illustrates that GCCs display differential responses according to their perceived risk of the threat (on-foot or drone approaches). Whilst on-foot monitoring methods remain effective when subjects are conspicuous, drones are more efficient and accurate for counting individuals in flocks, identifying nest site locations, and conducting egg and chick counts. The inclusion of drones as a monitoring tool for GCCs should thus be dependent on the aim of the study and budget requirements (equipment costs and legislative requirements). My results corroborate those of existing drone methodology studies, which suggest that it is not simply the employment of drones but how they are employed that makes them an effective data collection tool (Vas et al., 2015; Lyons et al., 2018; Weston et al., 2020; Mo & Bonatakis, 2022). Whilst this study may provide comprehensive guidelines for the research and monitoring of other large, threatened, and difficult-to-study waterbirds, utilising drones for wildlife monitoring is highly species-specific (Vas et al., 2015; Weimerskirch et al., 2018; Weston et al., 2020). I caution that future studies should first develop species-specific protocols before implementing drone methodologies.

Chapter 3: Breeding success and environmental correlates of endangered Grey Crowned Cranes (*Balearica regulorum*) in agricultural areas of KwaZulu-Natal, South Africa

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Dedication

"Conservation will ultimately boil down to rewarding the private landowner who conserves the public interest." – Aldo Leopold

I dedicate this chapter to the landowners in the Kokstad area. Some individuals whom I would like to thank and give recognition to specifically are Anne Louwrens, who expressed initial interest in my project and put me in contact with others; Mike and Jeanette Rennie, the most generous and kind-hearted hosts; Rory Bryden and Richard Mingay.

3.1 Title

Breeding success and environmental correlates of endangered Grey Crowned Cranes (*Balearica regulorum*) in agricultural areas of KwaZulu-Natal, South Africa.

3.2 Abstract

Birds are often used as ecological indicators because they are widely distributed across diverse habitats and display distinct behavioural responses to environmental changes. The endangered Grey Crowned Crane (*Balearica regulorum*) is an iconic species of wetland and grassland habitats, both of which are undergoing substantial transformation to alternative land-uses. The delayed reproductive strategies and habitat specialisation of Grey Crowned Cranes make them more vulnerable to extinction, but this risk is further compounded by data paucity. I employed traditional and contemporary methods to collect breeding metrics to determine this species' breeding success and to identify possible macro-environmental factors that promote or hinder their success in a key agricultural area in KwaZulu-Natal, South Africa. My results illustrate that Grey Crowned Cranes are sensitive to high rainfall intensity during the nesting stage but not during the hatchling/fledging stages. Multivariate analyses and multi-model inference revealed that successful nest sites were generally associated with larger open waterbodies, greater distances from shore, and increased proximity to secondary roads, buildings, and natural grasslands. Although increased agricultural activities might promote greater foraging opportunities, the overall breeding success of this species was low in this key agricultural region. The findings of this study stress the urgent need for further fine-scale data collection and monitoring activities, to better inform conservation actions for this species. I explicitly encourage future studies to focus on aspects affecting Grey Crowned Crane breeding in regions where proximity to human activities is inevitable.

Keywords: agriculture; disturbance; conservation; reproductive output; macro-environmental effects.

3.3 Introduction

Birds are exceptionally diverse and species-rich, occupying almost all habitats on Earth (Lees et al., 2022; Pillay et al., 2022). Since they demonstrate predictable responses to environmental changes in these wide-ranging habitats, they are considered useful ecological indicators (Fraixedas et al., 2020; Marcelino et al., 2020; Lees et al., 2022). For instance, if environmental shifts cause a misalignment of resources during key life stages, migratory species adjust their migration patterns (reaching destinations earlier or later than usual), while non-migratory bird species may attempt to shift their home range (Sillett et al., 2000; Visser et al., 2015; Teitelbaum et al., 2016). Climatic changes exacerbate these challenges whereby temperature variability and droughts delay insect emergence, affecting food availability (Charmantier & Gienapp, 2014). This can influence offspring growth and the opportunity to replenish the energetic costs that adults incur while breeding (Møller et al., 2008; Pearce-Higgins et al., 2010).

Larger birds with extended generation times, delayed reproduction, and greater dependence on specialised habitats face a higher extinction risk, especially if they cannot adapt to rapidly changing environments (Brown & Orians, 1970; Owens & Bennett, 2000; Ekman et al., 2004; Bird et al., 2020; Toussaint et al., 2021). The crane (Gruidae) family exhibits these traits and is one of the most threatened bird families globally (Beilfuss et al., 2007; Krajewski et al., 2010; Harris & Mirande, 2013). Most crane species traditionally rely on wetlands for breeding and grasslands for foraging (Beilfuss et al., 2007); however, commercial afforestation and agricultural intensification have transformed much of their natural habitat into timber plantations, pastures, and croplands (Morrison & Bothma, 1998; Weyer et al., 2015; Fakarayi et al., 2016; Wamiti et al., 2022). Although these landscapes provide greater foraging opportunities for cranes, a closer association with agriculture also increases their vulnerability to conflict with humans (Olupot, 2016; Austin et al., 2018; van Niekerk, 2018). Competing for similar resources in agricultural areas (Harris & Mirande, 2013; Fakarayi et al., 2016; Tilman et al., 2017; Amulike et al., 2020) has also led to increased reports of breeding failures following damming and drainage of wetlands, powerline electrocution and collisions, disease, and predation while poisoning, hunting, and illegal trading of these birds are also increasing (Bas et al., 2009; Harris & Mirande, 2013; Amulike et al., 2020; Galloway-Griesel et al., 2022).

A declining population's long-term persistence depends on an individual's reproductive output per breeding event (or lifetime) and the likelihood of their offspring reaching sexual maturity (De Villemereuil et al., 2019; Assersohn et al., 2021). Sub-Saharan Africa's most vulnerable crane species, the Grey Crowned Crane (*Balearica regulorum*, hereafter GCC) (Harris & Mirande, 2013), breeds during rainy seasons (high food availability) and produces among the largest clutch sizes of all crane species (Austin et al., 2018; Gichuki, 2000; Wamiti et al., 2022). Grey Crowned Cranes utilise synchronised parental incubation to guard eggs against aerial predators, while nesting in tall vegetation among inaccessible wetlands helps deter terrestrial predators (Wamiti et al., 2020; Wen et al., 2021). Despite all this, they are still experiencing major population declines. Although these nest selection preferences may effectively exclude natural predators from breeding sites, they also make it increasingly challenging to obtain accurate breeding metrics via traditional on-foot monitoring (Morrison, 1998), hindering conservation efforts. To better inform their conservation strategies (Soriano-Redondo et al., 2023), future studies should document nest site location and environmental factors that may directly or indirectly impact adults, eggs, or chicks, all of which ultimately influences breeding success (e.g., fluctuating incubation temperatures, food quality and availability, or protection – Wu et al., 2009; Wu et al., 2014; Wamiti et al., 2022).

To my knowledge, no study to date considers how the macro-environmental characteristics that surround GCC nest sites influence reproductive outcomes, and there remains a lack of comprehensive breeding data to determine this species' breeding success. This study aimed to address this by 1) determining the overall breeding success of this species, 2) identifying the reproductive stage at which GCCs are most at risk of reproductive failure, and 3) determining which macro-environmental factors (both anthropogenic and natural) influence breeding success across a range of land-use intensity sites in a key agricultural area in the southern Drakensberg, KwaZulu-Natal, South Africa. This study hypothesized that GCCs would exhibit a low overall breeding success. I further predicted that factors influencing hatching rate, a known vulnerability for many endangered species, would be a key contributor to this species' low reproductive output (Assersohn et al., 2021). Additionally, I anticipated that anthropogenic factors which disrupt breeding activities or alter breeding sites would be the primary macro-environmental determinants of low breeding success.

3.4 Methods and materials

3.4.1 Description of the study area

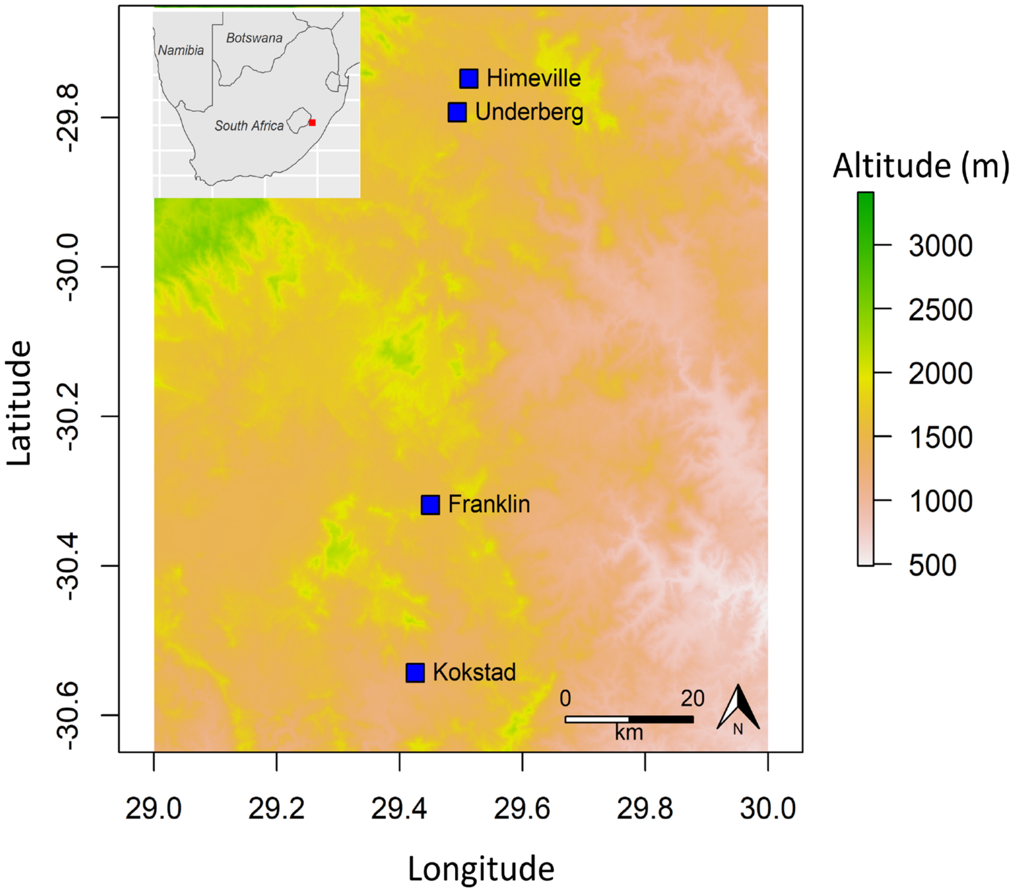

Figure 3.1: Distribution of study areas across an altitudinal gradient in the southern Drakensberg, KwaZulu-Natal, South Africa.

Nest site monitoring occurred in the southern regions of KwaZulu-Natal, South Africa, primarily in the Underberg, Himeville, Franklin, and Kokstad areas (Figure 3.1)[1]. This region receives an annual summer rainfall of between 650 and 1000 mm. However, during the 2022 – 2023 breeding season, this region experienced above-average rainfall attributed to a La Niña event (Jones, 2022). Indeed, rainfall data obtained from individual farmers in each study region indicated that precipitation during the 2022 – 2023 breeding season surpassed the yearly average recorded in previous years (Table 3.1). While open grasslands and wetlands are common in the southern regions of KwaZulu-Natal, the predominant land-uses in these areas are allocated to agriculture (intensive cropping and dairying, extensive beef, and sheep) and commercial forestry

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[1] Specific nest site locations have been omitted because this is potentially sensitive information that could be exploited by collectors, and I do not have the landowner's permission to share this information publicly.

(*Pinus spp.* and *Eucalyptus spp.*).

3.4.2 Data collection

Breeding success

During the 2022 – 2023 breeding season, I identified potential GCC breeding pairs using behavioural cues following Wamiti et al. (2020) – the primary indication of an active breeding site was that of a lone crane foraging near a waterbody, implying that its partner was at a nearby nest site. Because GCCs nest in difficult-to-access areas, I used a standard Mavic Air 2S drone (DJI Technology Co., Shenzhen, China) (595 g, 1-inch 20 MP sensor, 8× zoom, 65 dB low noise propeller) to monitor all nests following the GCC nest site approaching methodology detailed above (Figure 3.2).

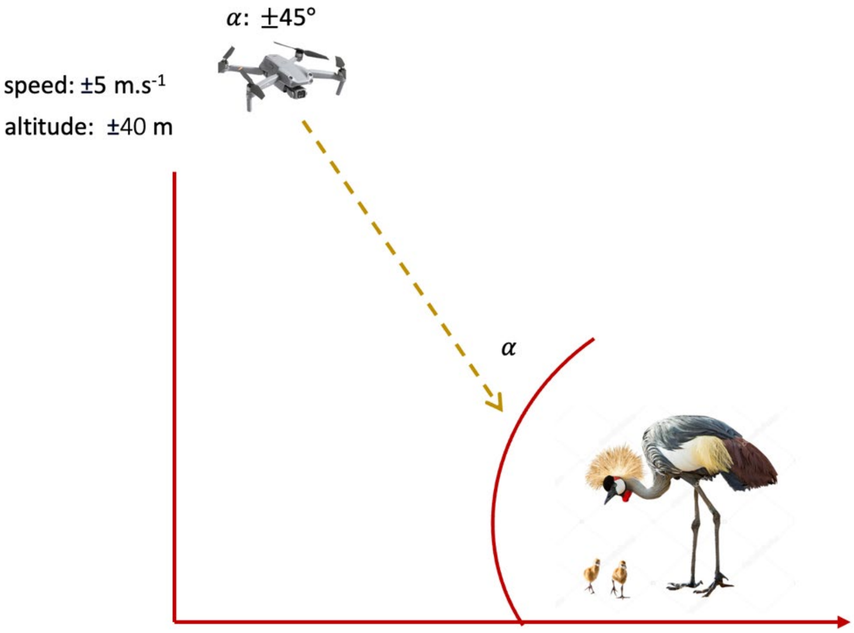

Figure 3.2: Schematic presentation of the general drone approach manoeuvre for monitoring GCC nest sites and family groups.

The number of drone flights during initial breeding stages (incubation and hatching) were kept to a minimum[2] to decrease disturbance and to lower the risk of nest or chick abandonment by parents. However, the small size and cryptic colouring of GCC hatchlings required closer and lower flights for accurate counts. Where possible, the

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[2] To account for potential variation in egg-laying timing, researchers should conduct a follow-up nest check one week after the initial flight, especially if only one egg was observed. This is particularly important for GCCs which can lay clutches of up to three eggs, with two-three days separating each egg. However, to minimize disturbance during the critical incubation period (28-31 days), no more than three nest visits should be conducted within this timeframe.

pilot used higher flights and the drone's zoom sensor to capture breeding metrics accurately. All flights involved cautiously manoeuvring the drone, approaching the pair and their chicks at an acute angle without hovering (spending ± 20 seconds at the nest). A schematic representation of the general approach manoeuvre is presented in Figure 3.2. Furthermore, video recording was enabled throughout the approach to facilitate *post-hoc* recording of breeding success metrics, thereby minimising monitoring time at nest sites.

A nest site was considered "active" if eggs were present or a crane was sitting on an identified nesting platform (i.e., incubating). If a pair displayed courtship behaviour but was not yet seen attending to a nest or chicks, the site was revisited at two-to-three-week intervals to determine whether the pair had progressed to a breeding attempt. During each breeding site observation, I counted the number of eggs, hatchlings, juveniles, and fledglings and differentiated between these stages based on their size and plumage. Distinguishing juveniles from fledglings was dependent on whether chicks could fly (whereby plumage development and fledging commonly take place 55 to 100 days after hatching – Gichuki, 2000). Throughout the breeding season, each nest site was revisited at two-to-three-week intervals from incubation until the offspring could fly or until there was no evidence of the family after two subsequent monitoring events. If a nest site was not monitored from incubation, it was excluded – since missing the initial nesting stage results in biases towards identifying nest sites that successfully hatch chicks and does not produce comprehensive breeding metrics (Jehle et al., 2004).

Nest site characteristics

Daily rainfall data for the 2022 – 2023 breeding season were sourced from local farmers who kept accurate records by measuring millimetres of rainfall with standard 10cm^2 rain gauges. These data were collected for each of the five regions where nest sites were situated. I also collected macro-environmental data describing the broader patch and landscape-scale habitat type around each nest site (Figure 3.3). I used GIS software to measure direct distances between the nest site and important environmental descriptors (i.e., nearest building, road, agricultural land, and water type) and to determine the dam and wetland surface areas (measured in square meters). The sole categorical descriptor, vegetation height, was categorised through *post-hoc* assessments using drone photographs taken within one meter of each nest site. The five vegetation height categories included "short" for grass, "medium" for reeds, and “tall” for bulrushes. Nest sites with a combination of these vegetation types were labelled as “short to medium” or “medium to tall.” Several of the chosen environmental descriptors were informed by prior research which highlighted their significance for describing the nesting habits of other wetland-nesting crane species (e.g., Ivey & Dugger, 2008; Wamiti et al., 2020; Gulati & Rana, 2021).

Breeding success metrics

Breeding success was assessed through three measures: 1) the total counts of offspring stages, 2) the probability of an offspring progressing from one stage to another (calculated as the total count in the subsequent stage divided by the total count in the previous stage), and 3) nest site success, determined when at least one juvenile or fledgling was observed. The identification of families became challenging once chicks gained the ability to fly, as they exhibited increased mobility. Therefore, I considered a breeding attempt successful when the offspring reached the juvenile/ fledging stage. In most cases these subjects could fly (i.e., between 80 and 140 days after hatching; see Figure 3.6 B) but had not yet left their parents or the area in which

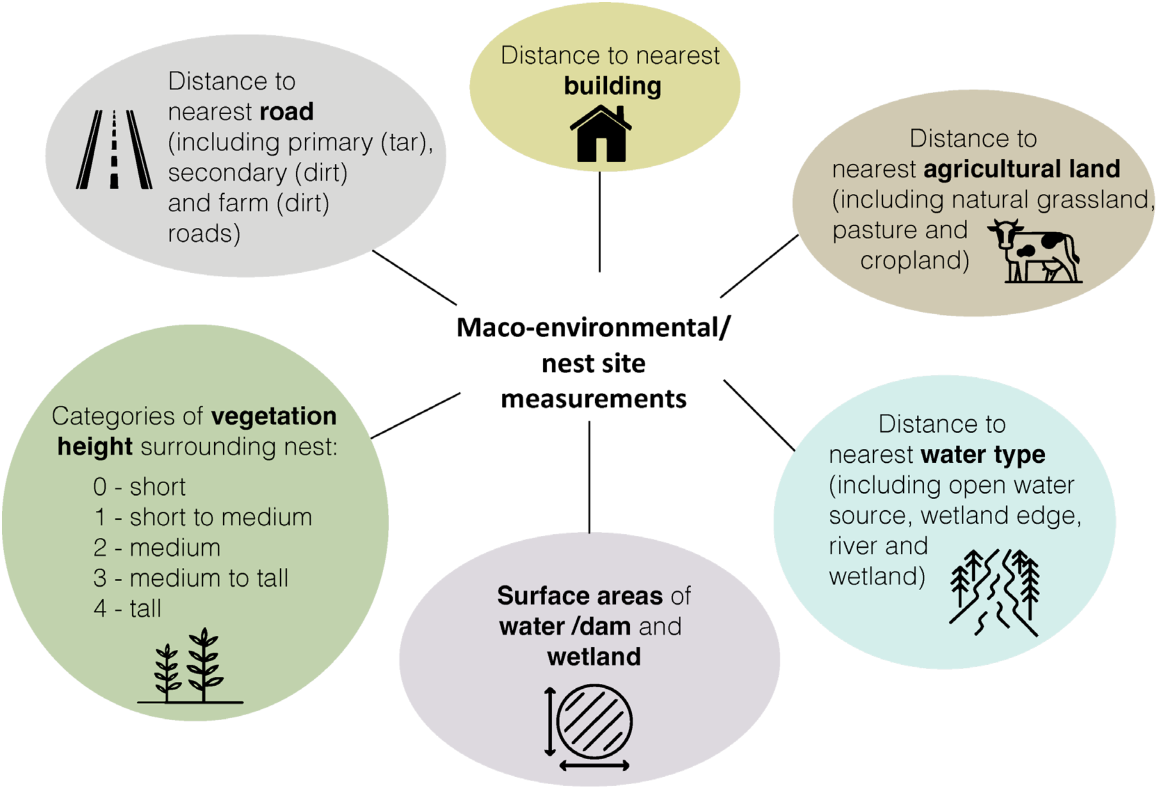

Figure 3.3: Visual representation of the macro-environmental descriptors assessed for each nest site. Non-categorical descriptors, excluding dam and wetland surface areas (square meters), depict measurements between the nest sites and the closest identifiable point of interest (meters).

their parents nested. This typically included fledged chicks, but in some instances, families already joined nearby flocks shortly after chicks became more mobile, making it difficult to identify specific families.

3.4.3 Statistical analyses

All statistical analyses were conducted in R version 4.3.1 (R Core Team, 2022). A generalised linear model was used to evaluate the number of observations at each nest site, with the “region” serving as the independent variable. Residuals were modelled using a Poisson distribution, while using a log link function ensured a positive fit. I estimated the date (an integer with 1 denoting the first observation in the breeding season) at which each developmental stage was most likely to be detected by using a log-linear mixed effects model (using the “lmer” function from the lme4 package – Bates et al., 2015). The developmental stage (a factor with four levels: eggs, hatchlings < 3 weeks, juveniles 3 – 12 weeks, and fledglings > 12 weeks of age) and breeding outcome (factor with two levels: success, failure) were included as independent variables with their interaction. Since repeated observations took place at each nest site throughout the breeding season, I controlled for this in all the mixed effects models by including “nest site” as a random intercept.

Offspring counts were then predicted for each developmental stage using a generalised linear mixed effects model (GLMM – “glmer” function from the lme4 package) with “offspring counts” as the independent variable and “developmental stage” as the response variable. Residuals were modelled using a Poisson distribution and a log link function to ensure positive fits. I further assessed the change in the number of offspring through time by using a GLMM with a Poisson distribution and a log link function. The number of days since the initial observation of the breeding attempt was incorporated as a third-order polynomial covariate. The developmental stage, categorised into four levels (eggs, hatchlings, juveniles, and fledglings), was included as a factor, and the interaction between these two independent variables was also included.

The probability of transitioning from one stage to the next was assessed using a GLM with residuals modelled using a binomial distribution and a logit link function to ensure proportional fits. First, I evaluated the probability of the different transition types succeeding. These included three sequential transition types (eggs to hatchlings, hatchlings to juveniles, juveniles to fledglings). The egg to juvenile transition was added to this model as a measure of nest site success – the probability that an egg would result in a juvenile indicating the overall survival probability of an egg. I then determined whether all eggs would transition to juveniles, i.e., the chance of obtaining 100 % success at the nest site.

In a second model, I assessed how transition probabilities of two transition types (factor with two levels, namely eggs – hatchlings and hatchlings – juveniles) change across a gradient of rainfall intensity (covariate) and the interaction of these two. A GLMM with a binomial distribution and a logit link function was used to conduct this analysis. Rainfall intensity (mm.day^{-1}) was calculated as the sum of the daily rainfall during each transition divided by the number of days the transition took to complete. Higher values indicate greater rainfall in a shorter amount of time. Here, I included a random intercept of "region" to control for differences in total rainfall between the regions. There was also a difference in the mean rainfall intensity experienced during these two transition types ($\chi^2 = 17.366$, df = 1, $p < 0.001$) and months ($F_{7,1236} = 340.34$, p < 0.001, Figure 3.4) – since rainfall intensity was greater earlier in the breeding season. This was controlled for by incorporating a random slope effect of rainfall intensity within months to capture the variable rainfall intensity observed between the months. Juvenile to fledgling transitions did not occur in all regions, so this transition was excluded from this analysis. Unless otherwise stated, all results from these regression models are presented as means ± 95 % confidence intervals (CI). Unless otherwise stated, significance was determined at $p < 0.05$.

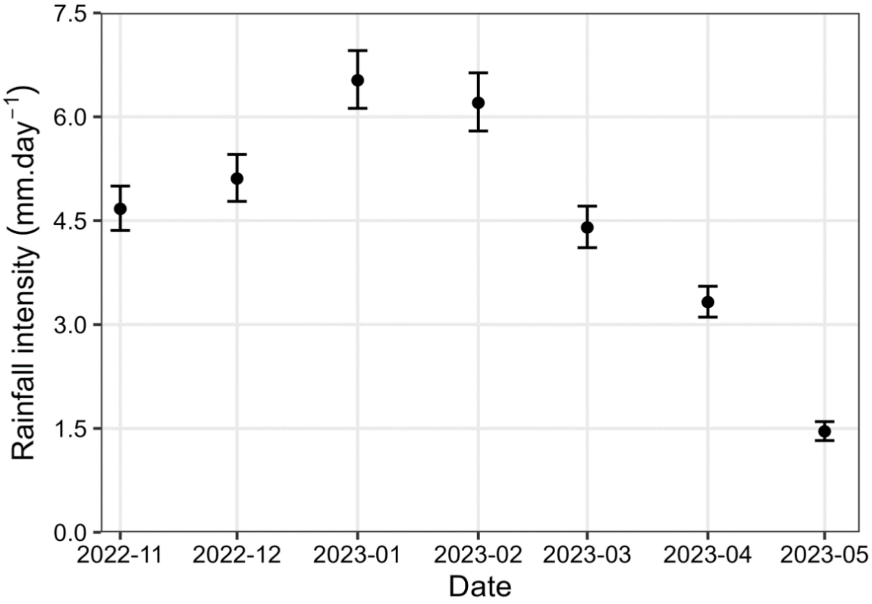

Figure 3.4: Rolling 30 – day rainfall intensity (mean ± 95 % confidence interval) across the 2022 – 2023 Grey Crowned Crane breeding season.

The biophysical descriptors collected for each nest site were used to explore trends in GCC breeding success using a principal components analysis (PCA). As the environmental descriptors differed by orders of magnitude, these measurements were log (x + 1) transformed and then standardised by dividing each measurement by the maximum transformed distance recorded for that measurement type to scale each measurement between zero and one. The PCA was then conducted using the “rda” function from the vegan package (Oksanen et al., 2022). I tested for the separation of centroids between successful and unsuccessful hatchings (hatching success) and the production of juveniles (overall success) by implementing analysis of variance using distance matrices (from the “adonis2” function in the vegan package). Euclidean distances were used in this analysis. Centroids and 95 % confidence envelopes were extracted from the “ordiplot” and “ordiellipse” functions from the vegan package for plotting purposes.

Using multi-model inference to complement the multivariate analyses, I identified the most important environmental descriptors, beginning with a complete model including all main effects. Models with all possible combinations of predictor variables were then assessed using the “dredge” function from the MuMIn package (Bartoń, 2023). The best-performing model of all the models within two AIC (Akaike information criterion) units of the best performing model (ΔAIC ≤ 2) was selected. To reduce the influence of potentially non-significant parameters included in these selected models, I applied a model averaging procedure using the “model.avg” function from the MuMIn package (Arnold, 2010). Since there is a strong correlation between likelihood ratio tests and ΔAIC with ΔAIC = 2 (translating to a confidence level of $p < 0.157$ as opposed to the more conservative $p < 0.05$ – Arnold, 2010), I report both the 95 % and 85 % confidence intervals (with 85 % confidence intervals being approximately equivalent to $p < 0.157$) in the final averaged model’s presentation for these analyses (Arnold, 2010; Sutherland et al., 2023). If a parameter was significant at the 85 % and not the 95 % level, I referred to this as a “moderately significant” effect.

For both the multivariate and the multi-model inference analyses, a nest site was considered to have successfully hatched offspring if at least one egg hatched. Similarly, a nest site was considered successful overall if at least one juvenile was observed at the nest.

3.5 Results

Ninety-five nests were identified and monitored across the five regions during the 2022 – 2023 breeding season (Table 3.1). On average, each nest site was observed 3.72 (3.44, 4.00) times, totalling 351 observations across all 95 nest sites. These observations were equally distributed across nest sites (i.e., no difference between sites: $\chi^2 = 3.238$, df = 4, $p = 0.519$, Table 3.1), showing no bias in nest site selection and monitoring. Rainfall intensity varied across regions, with Himeville recording the greatest rainfall intensity and Kokstad the lowest rainfall intensity ($F_{4,1239} = 2.523$, $p = 0.039$, Table 3.1).

Table 3.1: Description of data collection (counts and means (95 % confidence intervals) and rainfall amounts and intensities during the breeding season (Oct 2022 – May 2023) across different areas where GCC nest sites were identified. Rainfall intensity was measured over 10-day rolling periods throughout the observation period. Rainfall intensity results that share the same superscript letters indicate means that cannot be shown to be different.

Region	Number of nest sites	Observations per nest site	Rainfall (mm)	Rainfall intensity (mm.day^{-1})
Franklin	8	3.38 (2.31, 4.92)	906	2.88 (2.52, 3.28)^{ab}
Himeville	19	4.11 (3.29, 5.13)	1 192	3.54 (3.14, 3.98)^{a}
Kokstad	36	3.35 (2.81, 4.00)	697	2.73 (2.38, 3.11)^{b}
Underberg West	24	4.08 (3.35, 4.98)	1 054	3.19 (2.80, 3.62)^{ab}
Underberg East	8	3.62 (2.52, 5.22)	1 077	3.21 (2.82, 3.64)^{ab}

The average dates of observations throughout the breeding season (eggs, hatchlings, juveniles, and fledglings) are illustrated in Figure 3.5. These dates were significantly different between developmental stages ($F_{1,618.43} = 106.14$, $p < 0.001$) but did not differ between successful and unsuccessful nests ($F_{1,110.00} = 0.01$, $p = 0.913$). The interaction between these two variables was also non-significant ($F_{1,946.65} = 0.41$, $p = 0.666$).

3.5.1 Breeding outcomes

The number of individual offspring per nest differed between development stages, with significantly more eggs recorded than juveniles or fledglings ($\chi^2 = 27.079$, df = 3, $p < 0.001$, Figure 3.6A). The average number of eggs detected was 2.53 (2.30, 2.78). This average includes interesting observations of four nest sites, each with four eggs. The number of eggs continuously declined and were no longer detected after ± 30 days (estimated-df = 3.823, F = 70.69, $p < 0.001$). Hatchlings (estimated-df = 3.952, F =

29.19, $p < 0.001$), juveniles (estimated-df = 4.491, F = 23.26, $p < 0.001$), and fledglings (estimated-df = 3.129, F = 35.32, $p < 0.001$) all showed unimodal type responses with peak counts occurring at 24, 48 and 146 days, respectively (Figure 3.6B).

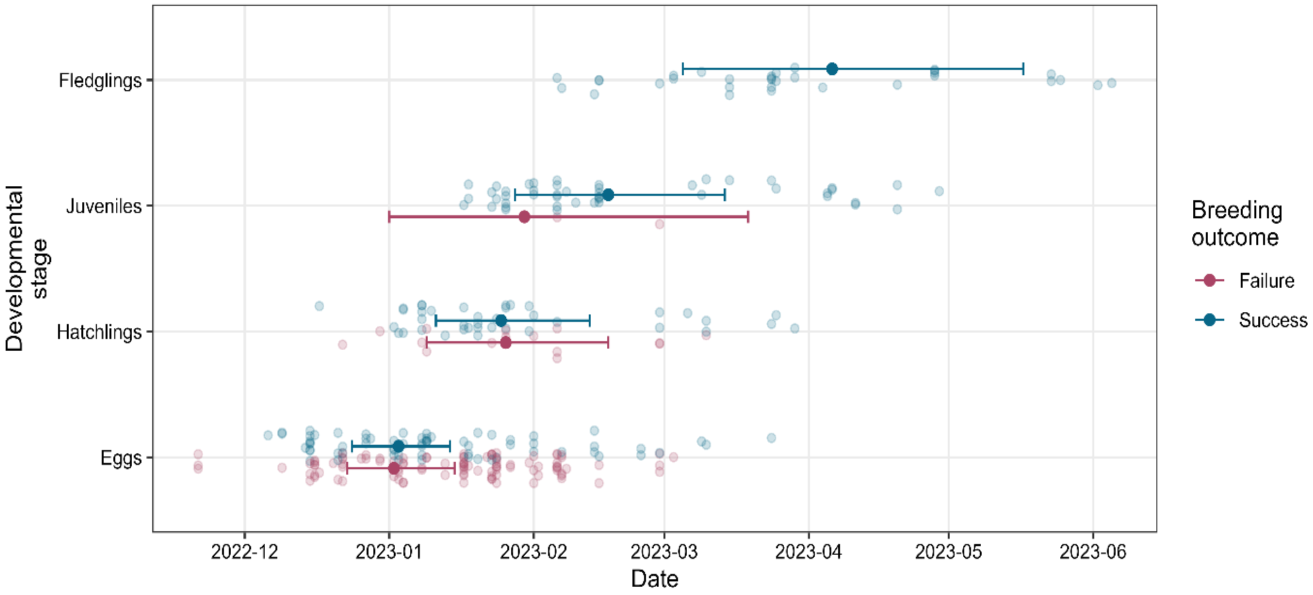

Figure 3.5: Mean (± 95 % confidence interval) date at which Grey Crowned Crane developmental stages were observed between successful and unsuccessful sites.

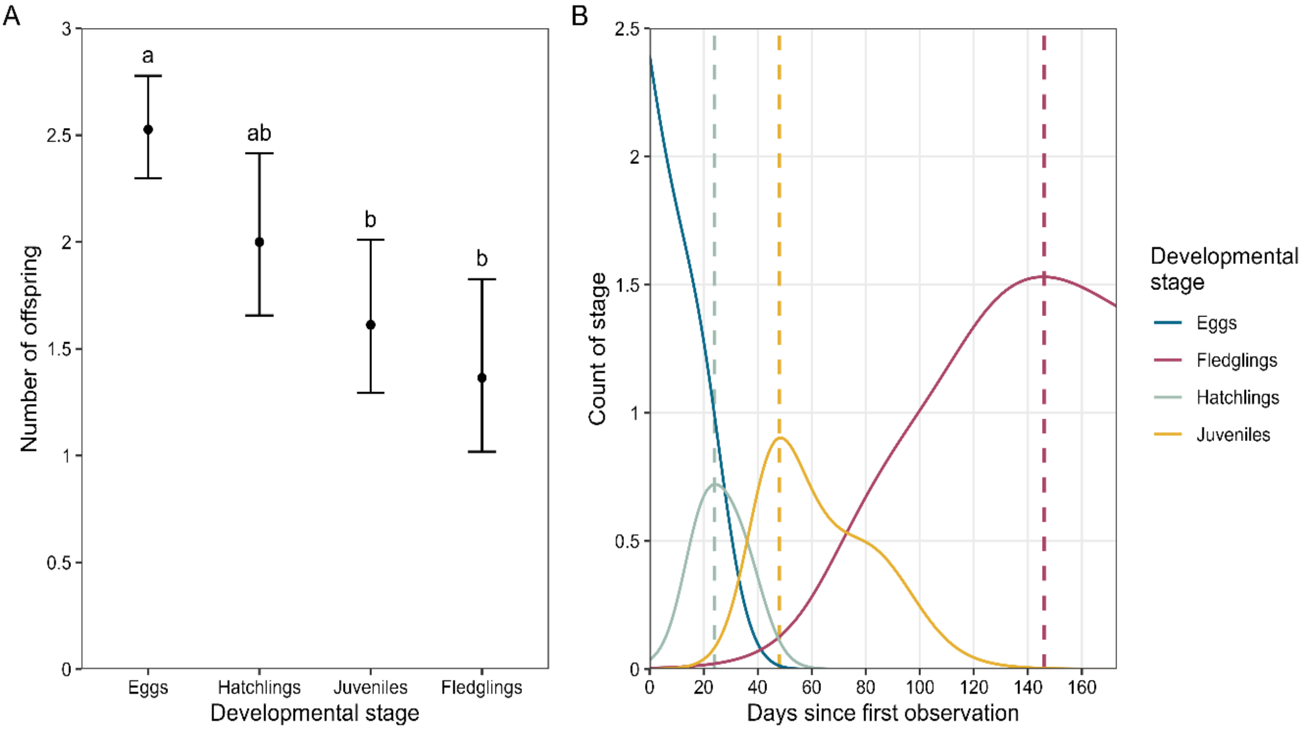

Figure 3.6: A) Number of Grey Crowned Crane offspring observed across the different developmental stages (mean ± 95 % confidence intervals). Shared letters denote that there is no evidence for significant differences. B) The number of observed offspring since the initial identification of the nest site. Dashed vertical lines represent the days at which the maximum number of offspring at a particular stage was observed.

3.5.2 Transition probabilities

The probability that a GCC would transition from one stage to the next differed significantly depending on the type of transition ($\chi^2 = 30.733$, df = 2, $p < 0.001$, Figure 3.7A). No significant difference was found in the probability of transitioning from eggs to hatchlings (38.4 (29.3; 48.4) %) in comparison to either transitioning from eggs to juveniles (31.1 (26.6; 36.1) %) or transitioning from juveniles to fledglings. However, transitioning from eggs to hatchlings was less likely to occur than the transition from hatchlings to juveniles (66.0 (52.1; 77.6) %), but the probability of transitioning from hatchlings to juveniles was not different from the probability of transitioning from juveniles to fledglings (59.0 (43.2; 73.1) %). Transitioning from eggs to juveniles was less frequent than transitioning from hatchlings to juveniles and from juveniles to fledglings. Furthermore, 10.6 (7.8; 14.2) % of nests showed a 100 % success rate where all eggs transitioned to juveniles – significantly less than all other transition types considered. By controlling for the general effect of rainfall intensity within the different regions, I found that the probability of developing from eggs into hatchlings was negatively affected by increased rainfall intensity ($\chi^2 = 4.071$, df = 1, p = 0.044, Figure

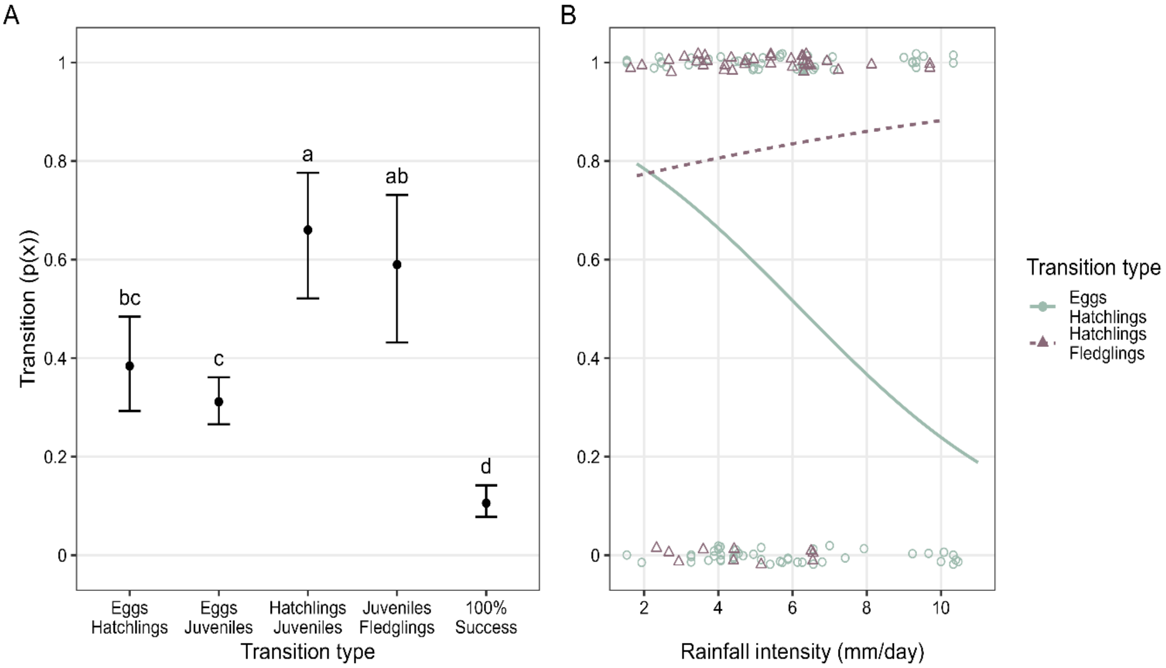

Figure 3.7: A) Probability of transitioning (mean ± 95 % confidence intervals) from one development stage to the next, where i) shared letters denote no difference, ii) “eggs-juveniles” explains the probability of an egg being successfully reared, and iii) “100 % success” indicates the probability of all eggs in each nest being raised successfully. B) Probability of transitioning from one stage to the next across a gradient of rainfall intensity (points are empty and jittered around p(x) = 0 or 1 to show overlap).

3.7B) but transitioning from hatchlings to fledglings was not (χ^2 = 0.0539, df = 1, p = 0.816, Figure 3.7B).

3.5.3 Breeding success

Principle component analysis revealed associations between the nest sites and environmental variables (Figure 3.8). The first principal component (PC1) explained 22.84 % of the variation in nest locations (eigenvalue: 0.16). It included wetland areas (21.2 %) and distances to buildings (16.0 %), water edge (15.6 %), tar roads (14.8 %), and farm roads (13.3 %) as the most closely related descriptors. The second principal component (PC2) explained 16.10 % of the variation (eigenvalue: 0.11) and represented distances to natural grassland (20.1 %), buildings (15.7 %), tar roads (14.8 %), rivers (11.9 %) and water edges (10.7 %). I found significant differences in the composition of nest site metrics when considering hatching success (PERMANOVA, 999 permutations, pseudo-F1,95 = 3.041, *p* = 0.006, Figure 3.8 – empty circles) but not in their overall success (PERMANOVA, 999 permutations, pseudo-F1,95 = 1.856, *p* = 0.073, Figure 3.8 – filled circles). These separations occurred along PC1.

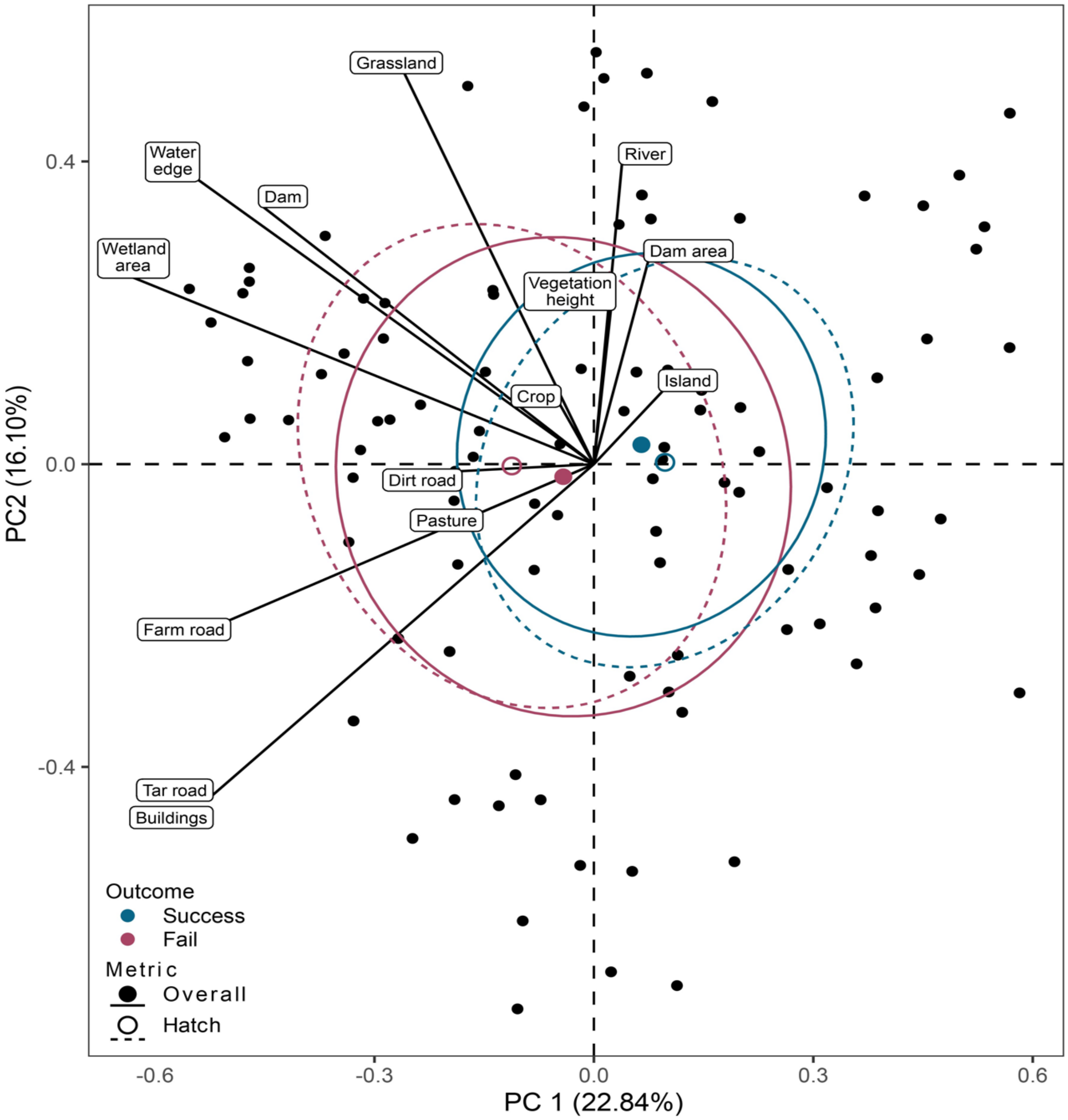

Figure 3.8: Plot of environmental descriptors of Grey Crowned Crane nest sites along axes one and two of a principal components analysis.[3]

Multi-model inference identified 11 candidate models to explain hatching success and eight models to define overall breeding success. Model averaging procedures applied to models where the ΔAICc was less than 2 (Figure 3.9; Table 3.2) revealed that hatching success decreased when nest sites were further away from natural grasslands and buildings. Moderate negative associations (significant at the 85 % but not 95 % level) with hatching success were also identified from increased distances to

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[3] Eigenvalues for PC1 and PC2 were 0.16 and 0.11, respectively. Black points represent the ordination of nest sites concerning the environmental descriptors. Larger, coloured points indicate the centroids of either successful or failed nest sites. Envelopes represent the 95 % confidence interval. Dashed envelopes and empty points represent hatching success (whether at least one hatchling was observed at the nest site). Solid envelopes and filled points represent overall success (whether at least one juvenile was observed at the nest site). All descriptors are distance metrics except for island, which indicates the presence of a nest on an island, and vegetation height, which represents the vegetation height class around the nest site.

dirt roads. Considering overall success, nest sites further away from buildings were less successful, while the reduced distance to natural grasslands was moderately associated with increased breeding success. Overall breeding success also had a moderately positive association with larger nearby dam surface areas.

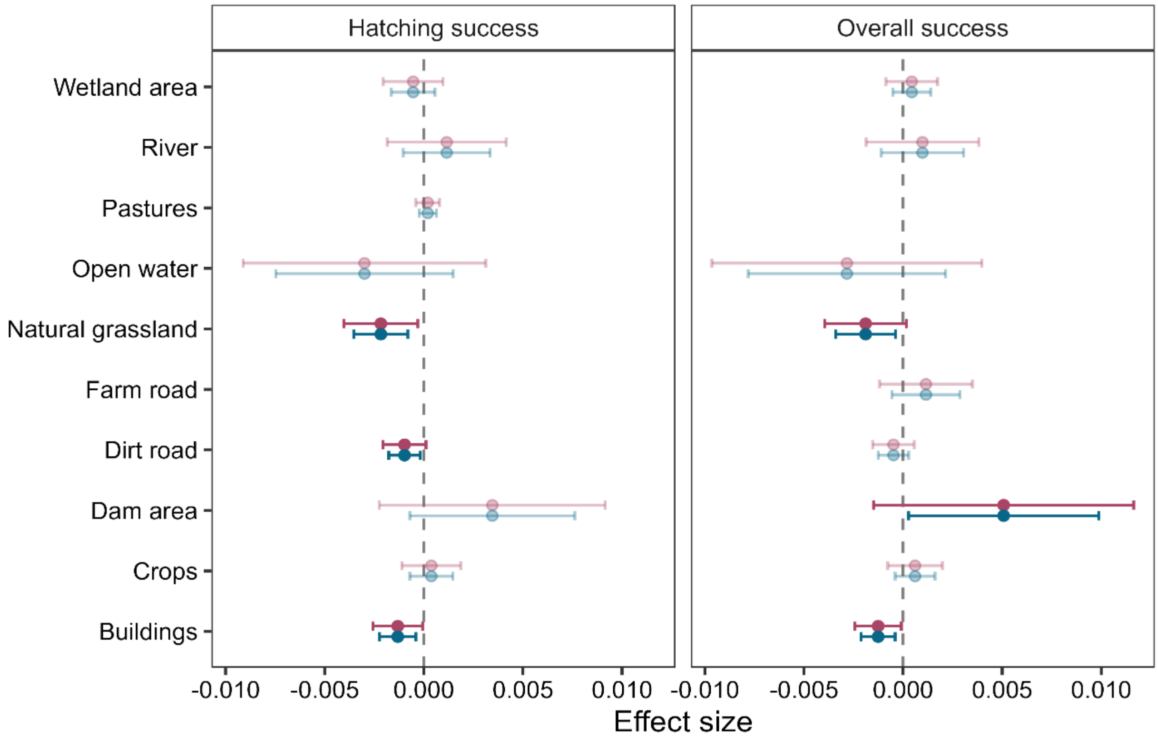

Figure 3.9: Model averaged effect sizes. Response variables represent distances from nest sites to the point of interest in meters for all covariates except for wetland area and dam area, which are measured in $m^2/1000$. Positive effect sizes represent a positive relationship between increased distance between the nest site and the point of interest (or size of wetland or dam) and increased nest site success. Negative effect sizes represent a negative relationship between increased distance between the nest site and the point of interest (or increased size of wetland or dam) and decreased nest site success.[4]

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[4] Error bars indicate 95 % (red) and 85 % (blue) confidence intervals. A dashed vertical line indicates no effect. Shaded effect sizes are non-significant at the $p < 0.157$ level (representative of ΔAIC = 2).

Table 3.2: Summary of the model selection procedure applied to hatching and overall breeding success. Only models with an ΔAICc <= 2 are included. For each model, we reported the model formula, the model's degrees of freedom (df), the log-likelihood (log(L)), the AICc criterion, ΔAICci = AICci – minAICc, Akaike weight (Weight). Models are ordered according to ΔAICc. LL – Log likelihood.

	Model	df	LL	AICc	Δ AICc	Weight
Hatching success	natural_grassland+dam_area+buildings+dirt_road	5	-55.5	121.8	0	0.18
	natural_grassland+buildings+dirt_road	4	-57.2	122.7	0.99	0.11
	natural_grassland+dam_area+buildings	4	-57.2	122.8	1.09	0.104
	natural_grassland+buildings	3	-58.5	123.2	1.47	0.086
	natural_grassland+dam_area+buildings+dirt_road+open_water	6	-55.1	123.2	1.47	0.086
	pasture+natural_grassland+dam_area+buildings+dirt_road	6	-55.2	123.4	1.67	0.078
	natural_grassland+dam_area+buildings+dirt_road+river	6	-55.2	123.4	1.67	0.078
	natural_grassland+dam_area+wetland_area+buildings+dirt_road	6	-55.3	123.5	1.73	0.076
	natural_grassland+buildings+dirt_road+open_water	5	-56.5	123.7	1.92	0.069
	natural_grassland+dam_area+dirt_road	4	-57.6	123.7	1.95	0.068
	crops+natural_grassland+dam_area+buildings+dirt_road	6	-55.4	123.8	2	0.066
Overall success	natural_grassland+dam_area+buildings	4	-56.2	120.9	0	0.234
	natural_grassland+dam_area+buildings+farm_road	5	-55.8	122.2	1.26	0.125
	natural_grassland+dam_area+buildings+dirt_road	5	-55.8	122.3	1.38	0.117
	crops+natural_grassland+dam_area+buildings	5	-55.8	122.3	1.38	0.117
	natural_grassland+dam_area+buildings+open_water	5	-55.9	122.4	1.48	0.112
	dam_area+buildings	3	-58.2	122.6	1.66	0.102
	natural_grassland+dam_area+buildings+river	5	-56	122.7	1.76	0.097
	natural_grassland+dam_area+wetland_area+buildings	5	-56	122.7	1.79	0.096

3.6 Discussion

3.6.1 Overview of breeding outcomes

The distribution of any species is ultimately dictated by the availability and accessibility of critical resources (Wiens, 2011). For crane species facing resource scarcity within protected areas, survival often hinges on venturing into unprotected zones to meet their needs (Austin et al., 2018). However, reviving declining crane populations in these unprotected areas is highly dependent on successful breeding outcomes within the species, which commonly necessitates adaptation to changing environments (Charmantier & Gienapp, 2014; Wamiti et al., 2022). Non-migratory species (e.g., GCC) cannot easily shift their home range to preferable environmental conditions or land-use types (Ramírez et al., 2018; Donnelly et al., 2022), which increases their reliance on habitats in unprotected areas (Burnham et al., 2017; Hemminger et al., 2022). Therefore, implementing effective conservation strategies to assist private landowners in conservation management requires a deeper understanding of a species' utilisation of the habitat and, concerning breeding, understanding their current breeding outcomes and the possible factors hindering or promoting breeding success.

To the best of my knowledge, this study is the first to employ a drone to successfully monitor GCC nest sites in largely unprotected landscapes. In a single breeding season, 95 nest sites were consistently monitored, which is substantially higher than what has been achieved with traditional on-foot monitoring methods (e.g., Wamiti et al. (2022) managed to monitor 33 out of a possible 63 active GCC nest sites by on-foot wading to nests). Throughout these monitoring events, I found that a) the typical GCC clutch size consisted of approximately 2.5 eggs, aligning with findings from GCC clutch sizes in Kenya (Wamiti et al., 2022); b) the most sensitive stage of GCC breeding was their hatching stage which was affected by several environmental and climatic factors; and c) the low overall breeding success of this species emphasises the need for improved conservation strategies aimed at improving this species' hatching rate.

3.6.2 Hatching and fledging rates

Several studies suggest that the reproductive success of cranes increases when monogamous pairs become more familiar with one another through frequent socialising, which also strengthens pair bonds and matures their breeding experience (Ivey & Dugger, 2008; Hammers et al., 2012; Teitelbaum et al., 2017; Barwisch et al., 2022). However, gaining experience takes time and increases this family's extinction risk (Stevens & Conway, 2020). One of the most common conservation challenges of stagnant or declining populations of threatened bird species is the failure of eggs to hatch (Assersohn et al., 2021). Previous GCC hatching rates in Kenya were 83.6 % (Gichuki, 1993) and 91.3 % in Ethiopia for Black Crowned Cranes (Zelelew et al., 2019), but both inferred a low overall breeding success since less than half of the clutches in their study fledged. I observed a substantially lower hatching rate than these earlier studies with only 38.4 % of eggs hatching, 66.0 % of hatchlings transitioning into the juvenile stage, and 59.0 % of juveniles surviving to the fledging stage. These findings suggest that the nesting phase represents the most susceptible period in GCC breeding, aligning with the concern previously expressed by Assersohn et al. (2021). After hatching, crane chicks remain vulnerable to predation and environmental challenges for 75 – 90 days until they fledge. The likelihood of chick survival typically rises as they mature and become more adept at identifying threats and evading predators themselves (Fox et al., 2019).

3.6.3 Transition stages

Unlike other species, which only invest parental care in one of two hatchlings (e.g., Wattled Cranes *Bugeranus carunculatus*), GCCs attempt to raise all hatchlings (Morrison & Bothma, 1998; Morrison, 2015; Zelelew et al., 2019). This supports my findings, demonstrating that 10.6 % of GCC pairs managed to raise all eggs in their clutch until the fledging stage. The transition probability of GCC hatchlings to juveniles/fledglings (one to two fledglings per pair) was also higher than that of other crane species. For example, Wattled Cranes in Mozambique produced 0.42 chicks per pair in 1999 and ± 0.25 chicks per pair in the two wetter years that followed (Bento et al., 2007). During an eight-year study on the critically endangered Whooping Crane (Grus americana), another investigation reported a 30 % hatching rate, with 47 % of these hatchlings surviving until the fledging stage (Spalding et al., 2009). This equates to an overall breeding success of approximately 14 %. Subsequent studies emphasised that the recovery of this critically endangered species is highly dependent on their ability to improve their low breeding outcomes (Butler et al., 2017). Although the transition probabilities of GCC were higher than those of the Whooping Crane, their overall breeding success remains comparable. Consequently, my findings support the 2012 IUCN up-listing of GCCs to an “Endangered” status.

3.6.4 Rainfall interactions

Breeding birds incur high energetic costs when defending territories, incubating eggs, and raising young (Gichuki, 2000; Geldart et al., 2022). However, these costs are even higher during suboptimal environmental conditions, which are predicted to become more frequent (i.e., droughts and high rainfall in alternating years – Marcelino et al., 2020; Connell et al., 2021). While rainfall generally enhances avian breeding success by optimising habitat conditions (Woolley et al., 2022), prolonged and heavy rain (especially over a short period) may lead to flooding or cooler weather and wet nest conditions, affecting the temperature of the eggs (Ivey & Dugger, 2008). Maintaining egg temperature is especially important for species where both sexes share incubation duties (including most crane species), as eggs are regularly exposed to varying ambient temperature extremes and predators during rotation (Ivey & Dugger, 2008; Du Rant et al., 2013). My results indicate that the incubation phase (eggs) experienced greater vulnerability than hatchlings when exposed to intense rainfall. Furthermore, I noted instances of nest abandonment by GCCs shortly after heavy rainfall and hail events (Demmer, pers. obs.). Similar observations have been made with Greater Sandhill Cranes (*Antigone canadensis tabida*), which abandoned flooded nests following high rainfall events (> 50 mm of rain within 24 h), leading to a significant number of nest failures (Nesbitt, 1988; Fox et al., 2019).

Interestingly, several crane species tend to renest after initial failed breeding attempts (Nesbitt, 1988; Thompson et al., 2022; Woolley et al., 2022). However, the decision to renest depends on various factors, including the time available to renest, environmental conditions and parental body conditions, and the species' breeding strategy (Saalfeld et al., 2021). While renesting efforts have improved the breeding success in various bird families (e.g., family Gruidae – Hayes, 2022 and family Laridae – Ledwoń et al., 2023), this trend also has exceptions (Jones et al., 1995). For example, threatened Piping Plovers (*Charadrius melodus*) produce smaller and less successful clutches from renesting events than those from their initial breeding attempt. Frequent renesting can also lead to the bird's energetic costs outweighing their long-term reproductive success (Swift et al., 2020). I noted some (*n* = 4 – excluded from analyses in this study) renesting attempts among breeding pairs after initial failures (suspected to have failed because of flooding). These pairs commonly renested near (30 – 500 m) initial nest sites, or closer to locations where water entered the waterbody, perhaps to reduce the risk of subsequent flooding. Either way, pairs usually stayed or renested within the same area as their initial breeding attempt (Demmer, pers. obs) but likely in a new territory (i.e., Wamiti et al. (2022) considered the distance between any two active nests as the minimum territory size which they found to be about 47 m in their study area). While success was observed in some cases, others attempted renesting later in the breeding season when rainfall was low, and temperatures were considerably cooler (showing no shift in breeding strategies or attempts in anticipation of the risks of higher rainfall). Delayed renesting may have led to a mismatch between resource requirements and the vulnerable developmental stage of their chicks (as reported by Zelelew et al., 2019 and Martay et al., 2023). Nevertheless, I acknowledge that this study was limited to a single breeding season, and future investigations could provide insights into i) potential variations in breeding strategies of GCCs across seasons in response to long-term climatic changes and ii) the impact of renesting attempts on the overall breeding success of this species.

3.6.5 Macro-environmental conditions

Meine and Archibald, (1996) theorised that the generalised foraging behaviour of GCCs might be advantageous for adapting to future habitat changes. Subsequent research has shown that several crane species benefit from increased foraging opportunities after cropping seasons in agricultural landscapes (Austin et al., 2018). The ability of cranes to pass learned behaviours from experienced to non-experienced individuals (the phenomenal cultural transmission) may partially explain why more cranes are taking advantage of more accessible foraging opportunities in agricultural landscapes (Hayes & Barzen, 2016; Teitelbaum et al., 2019). However, despite the benefits of increased foraging opportunities, the intensity of agricultural practices (e.g., grazing, cropping, and damming – Dalu et al., 2017) drastically transforms natural ecosystems, modifying sensitive breeding habitats (Bartzen et al., 2010; Sica et al., 2018). The close nesting proximity to human disturbances during vulnerable and energetically taxing breeding stages (e.g., incubation) may also lower breeding success (Olupot, 2016; Seress et al., 2020; Geldart et al., 2022). This is supported by observations of the migratory White-naped Cranes (*Grus vipio*), which have continuously been shifting their nest sites further away from disturbances such as roads and settlements (Wu et al., 2014).

When species shift breeding grounds towards human disturbances, it may suggest decreased suitability of breeding habitats (Fox et al., 2019), forcing birds to select nest sites in less optimal locations (also observed in cranes – Lacy et al., 2015). A second suggestion implies a certain tolerance level to, if not a preference for, certain human disturbances (Meine & Archibald, 1996 and Wamiti et al., 2022 infer that this may be the case for the GCCs). I found that GCCs nesting closer to disturbances (secondary roads and buildings) enhanced the hatching success of GCCs. I believe this may be in response to habitat loss and some level of preference for nesting in these landscapes. Other crane species have also shown hatching success in highly disturbed areas, with their characteristically smaller clutch sizes (in comparison to other bird species) and increased parental care being seemingly beneficial in these environments (e.g., Ge et al., 2011; Wang et al., 2011; Li et al., 2015). However, a closer association with agriculture exposes cranes to natural predators. This study did not assess predator presence around nest sites. However, predation via natural predators is an ongoing challenge for ground-nesting birds that inhabit farmland landscapes (Bravo et al., 2023) and may help explain some of the associations reported here. I observed and received reports from landowners of some predatory incidences on GCCs (*n* = 6, Demmer, pers. obs.) by generalist meso-predators (serval *Leptailurus serval* and jackal *Lupulella mesomelas*). These predators are commonly associated with intensively managed pastures during calving and lambing seasons (Drouilly et al., 2018). This may help explain the positive association between GCC breeding success and closer proximity to natural grasslands where such predators are assumed to occur in lower numbers given the lower overall prey densities in those habitats.

Wu et al. (2014) provide a summary of comprehensive research on bird habitat selection, concluding that the perception of habitat availability and the concept of habitat selection are influenced by spatial scale. I found some strong associations with other environmental factors apart from rainfall. Nesting on islands, for example, is common in several waterbird species (e.g., Burgess and Hirons, 1992; Scarton and Valle, 2020) and was also utilised among GCCs. Multivariate analyses suggested an association of greater breeding success when nest sites occurred on islands, with a lower risk of terrestrial predation likely contributing to this success. Previous studies indicate that GCCs commonly locate their nest sites in moderate (50 cm) water depth amongst taller (60 – 90 cm) vegetation that is further away (100 m) from shore (Wamiti et al., 2020). Most nest sites in this study were surrounded by tall vegetation, likely to conceal nest sites from terrestrial predators (Olupot, 2016). Yet, my results indicate that vegetation height did not necessarily promote reproductive success. Although anecdotal, I observed three instances when birds of prey were at nests, feeding on exposed eggs during nest site monitoring (Demmer, pers. obs.). As birds of prey approach from above, tall vegetation has little effect in concealing the nest site. This could explain why vegetation height was found to be unimportant concerning breeding success. Finally, nest sites situated in waterbodies with larger surface areas improved overall breeding success – likely because large, healthy waterbodies act as biodiversity hotspots, meeting a greater number of habitat requirements for significant life events of inhabiting species (Creed et al., 2017; Li et al., 2019; Toussaint et al., 2021; Donnelly et al., 2022).

3.6.6 Conclusions

In conclusion, this study provided fundamental insights into the breeding success of GCCs in unprotected areas. It has highlighted a significant attrition rate in GCCs between the egg and hatchling stages and confirmed that macro-environmental factors surrounding nest sites influence the success or failure of a nest. Notably, this study highlights the capability of GCCs to successfully rear young in agricultural landscapes, suggesting that improvements to this species’ breeding success in non-traditional environments with increased disturbances are possible. However, achieving this will necessitate greater collaboration between conservation initiatives and private landowners, emphasising the preservation of existing nest sites. It is crucial to recognise that the degradation of critical nesting locations outweighs any foraging benefits and threatens future breeding opportunities. I also advocate for a greater focus on implementing effective monitoring methods and regularly collecting and communicating data. This approach will contribute to informed decisions regarding ecosystem health and land-use management and play a pivotal role in sustaining the breeding opportunities of this endangered species.

Chapter 4: Synthesis, conclusions and recommendations

This chapter concludes this study by reviewing my key research findings in relation to the research aims and questions, while considering the value and contribution of these findings to crane ecology and conservation. I also evaluate this study's limitations and provide suggestions for future research.

4.1 Research findings in relation to research aims and questions

In Chapter 1 I identified fundamental knowledge gaps relating to the monitoring and breeding of the endangered Grey Crowned Crane (GCC). Land-use changes within key GCC habitats pose a continuous threat to population sustainability. These changes, coupled with the isolated nature of GCC populations and their specific breeding habits, hinder our ability to accurately assess population trends. Therefore, developing more effective monitoring methods to gather precise data on breeding success is crucial to inform future conservation strategies. Through extensive experimental investigation, the findings presented in Chapter 2 suggest that drones can be used as an effective ecological monitoring tool for all three GCC groupings (pairs, families, and flocks). Drones were able to approach groupings at significantly closer distances compared with on-foot monitoring. In this context, nesting birds exhibited less evasive behaviour in response to drone flight heights when compared with flocks. However, they were more responsive to drone approach angles at certain stages of their breeding process. The findings of this experimental investigation also helped inform guidelines that focus on using drones to collect breeding metrics at nest sites located among tall, inaccessible wetland vegetation. Following these guidelines, I used a drone to collect breeding metrics from 95 GCC nest sites throughout a single breeding season in a key agricultural area in KwaZulu-Natal (Chapter 3). I found that GCCs displayed a low hatching rate, while climatic and environmental factors also influenced their breeding success. Interestingly, nest sites located closer to human presence were associated with more positive breeding outcomes, suggesting that GCCs show some tolerance to certain anthropogenic conditions.

4.2 Limitations and future recommendations

This study successfully met its intended objectives, but it is important to contemplate its potential limitations along with key aspects that could be explored in future studies. Since informed conservation strategies hinge on accurate data collection and comprehensive conclusions, my primary suggestion is to refine the efforts of this study in developing the first species-specific drone guidelines for monitoring GCCs. I also encourage subsequent studies to focus on wetland nesting cranes since several aspects of GCC breeding still require further investigation. Secondly, this study was temporally restricted to a single breeding season, which experienced a higher-than-average rainfall intensity. While the sample size used to determine GCC breeding success was adequate, future studies are encouraged to replicate this study over a longer period to better understand this species' breeding during extreme and non-extreme climatic seasons. Another important aspect may include exploring whether GCCs display flexibility in their breeding strategies since such flexibility might help them overcome reproductive losses during abnormal climatic events. Finally, some anecdotal observations might also prove useful for future research. For example, I observed more predation incidences by land predators during the agricultural calving and lambing season, which partly overlaps with periods when GCC chicks have not yet fledged and are thus more vulnerable. Conservation strategies may benefit from understanding how local predation might influence breeding success, particularly in areas with increased human activity.

In considering possible improvements for the effective conservation of these endangered birds, it is important to highlight that extensive collaboration with private landowners was pivotal to the findings of this project. Efforts relating to this aspect included informing, creating interest amongst, and encouraging landowners to safeguard existing wetland nest sites through better land-use practices. Prioritising these relationships ignited a notable enthusiasm for crane conservation among these landowners and other community members, which further initiated subtle changes to farming practices at several study sites. Though my findings suggest an apparent adaptability of GCCs to intensive agriculture, I reiterate the detrimental contribution of habitat loss to this species' declining population. Consequently, future collaborative conservation efforts should discourage modifications or interference at wetlands, as these disruptions are likely to impact nest site availability and decrease egg-hatching rates, ultimately hindering the long-term population recovery of this species. On the contrary, conservation groups and governmental bodies could acknowledge and incentivise (e.g., through certificates of recognition) farmers who make efforts to aid in the conservation of globally endangered species.

4.3 Conclusions

In summary, this research study addressed fundamental knowledge gaps in this species. It has also provided a foundation for future research and conservation initiatives to implement precise, efficient, and budget-friendly methods for monitoring GCCs and informing their conservation initiatives. Given that cranes primarily inhabit unprotected landscapes, sustaining crane populations relies heavily on private landowners. In many cases, these landowners have played a crucial role in artificially supporting declining crane populations. Thus, the continued existence of this species, along with many other endangered species, relies on constructive collaboration with private landowners, careful monitoring, and effective conservation strategies that balance the inevitable pressures from human and economic development.

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