Environmental correlates of breeding outcomes in Endangered Grey Crowned Cranes *Balearica regulorum* in agricultural areas of KwaZulu-Natal, South Africa

Research Article

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Summary

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 regarded as a flagship species of Africa's wetland and grassland habitats, both of which are undergoing substantial transformation to alternative land uses. The delayed reproductive strategies and habitat specialisation of this crane species makes them more vulnerable to extinction, but this risk is further compounded by data paucity. We employed traditional and contemporary survey methods to collect breeding metrics to calculate stage transition probabilities (i.e. egg–hatchling, hatchling–juvenile) and to identify possible macro-environmental factors that either promote or hinder their reproductive output in a key agricultural area in KwaZulu-Natal, South Africa. We found that Grey Crowned Cranes have a low hatching rate of 38.4% (95% confidence interval 29.3–48.4%) and show that this low hatching rate is exacerbated under high rainfall intensity. Multivariate analyses and multi-model inference revealed that successful nest-sites were generally associated with larger open water-bodies, 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 outcomes of this species were poor in this key agricultural region. Our findings stress the urgent need for further fine-scale data collection and monitoring activities to better inform conservation strategies for this species. We also encourage future studies to focus on aspects affecting Grey Crowned Crane breeding in regions where proximity to human activities is inevitable.

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Introduction

Birds are an exceptionally diverse class, occupying almost all habitats on Earth (Lees et al. 2022). However, many species are threatened due to anthropogenic activities, associated habitat loss and resulting competition between humans and birds for the same resources (Amulike et al. 2020; Fakarayi et al. 2016; Harris and Mirande 2013; Tilman et al. 2017). Birds display distinct behavioural changes in response to environmental changes, making them valuable ecological indicators (Fraixedas et al. 2020; Lees et al. 2022; Marcelino et al. 2020). For example, some environmental changes result in a mismatch of important resources or optimal conditions during key life stages, forcing migratory species to adjust their migration patterns (Sillett et al. 2000; Visser et al. 2015; Zurell et al. 2018), whilst non-migratory bird species attempt to shift their home ranges (Santisteban et al. 2012). Furthermore, delayed insect emergence and reduced food availability associated with climatic changes disrupt hatchling growth and extend the time it takes for adults to replenish the energetic costs incurred during breeding (Charmantier and Gienapp 2014; Møller et al. 2008; Pearce-Higgins et al. 2010).

Larger birds with longer generation times and delayed reproduction, as well as those that rely on specialised habitats, face a higher extinction risk, especially if they cannot adapt to changing environments (Bird et al. 2020; Brown and Orians 1970; Owens and Bennett 2000; Toussaint et al. 2021). Cranes (Gruidae) are among the most long-lived bird species, with generational lengths of approximately 12 years (vs the average of approximately three years for all bird species) (Bird et al. 2020; Zelelew et al. 2019). This, together with their habitat specialisations, magnifies their extinction risk (Edwards et al. 2022; Owens and Bennett 2000), making cranes among the most threatened bird families globally (Beilfuss et al. 2007; Harris and Mirande 2013). The Grey Crowned Crane *Balearica regulorum* is sub-Saharan Africa's most vulnerable crane species and was uplisted to "Endangered" on the International Union for Conservation of Nature (IUCN) Red List in 2012 (Harris and Mirande 2013). Grey

Crowned Cranes have a strong reliance on wetlands for breeding and grasslands for foraging (Beilfuss et al. 2007); however, commercial afforestation and agricultural intensification now expose this species to the risk of habitat loss (Fakarayi et al. 2016; Morrison and Bothma 1998; Wamiti et al. 2022; Weyer et al. 2015). The resulting close association of cranes and agriculture (Olupot 2016) is linked to increasing reports of breeding failures following damming and drainage of wetlands, powerline collisions, disease, and predation; while poisoning, hunting, and illegal trading of these birds are also increasing (Amulike et al. 2020; Galloway-Griesel et al. 2022; Harris and Mirande 2013).

The long-term persistence of a population, particularly in response to climate change, is directly related to an individual's reproductive output per breeding event or lifetime, as well as the probability that their offspring will reach sexual maturity (Assersohn et al. 2021). Grey Crowned Cranes breed during the summer rainy season when seeds and insects are abundant, a strategy which improves parent condition and chick survival (Austin et al. 2018; Gichuki 2000; Wamiti et al. 2022). Grey Crowned Cranes lay large clutches compared to other cranes (Wamiti et al. 2022), and their strategy of synchronised parental incubation assists with protecting eggs from aerial predators while nesting in tall, inaccessible wetlands offers concealment from terrestrial predators (Wamiti et al. 2020; Wen et al. 2021). These reproductive behaviours and nest-site preferences have made traditional on-foot data collection of breeding metrics challenging, resulting in data paucity and ineffective conservation planning for this species (Morrison 1998). More detailed metrics are needed to better understand the factors that directly or indirectly impact adults, eggs or chicks (e.g. through fluctuating incubation temperatures, food quality, and availability or protection from predators; Wu et al. 2014), ultimately impacting breeding success (Soriano-Redondo et al. 2023; Wamiti et al. 2022; Wu et al. 2009).

To our knowledge, no study has investigated how surrounding macro-environmental characteristics influence the reproductive outcomes of Grey Crowned Cranes, and the absence of extensive breeding data hinders our ability to determine the breeding outcomes of this species. Therefore, our study aimed to (1) determine the general breeding outcomes of this species in a key agricultural area in South Africa, (2) identify the stage where reproductive failure is most likely by assessing the transition probabilities between early life stages, and (3) understand how specific macro-environmental factors (both human-related and natural) affect reproductive outcomes.

Methods

Study area

Nest-site monitoring took place during the 2022/3 Grey Crowned Crane breeding season in the Underberg, Himeville, Franklin, and Kokstad regions of KwaZulu-Natal, South Africa (Figure 1). This summer-rainfall region (650–1,000 mm per annum) has large areas of open grasslands and wetlands while agriculture (intensive cropping and dairying, extensive beef and sheep) and commercial forestry (*Pinus* spp. and *Eucalyptus* spp.) are the primary land-use types occurring in these regions. Rainfall records supplied by farmers in each study region showed that rainfall during the 2022/3 breeding season exceeded the yearly average captured in previous years (Supplementary material Table S1), likely resulting from a La Niña event (Jones 2022).

Data collection

General breeding outcomes and transition probabilities

We identified potential Grey Crowned Crane breeding pairs using behavioural cues following Wamiti et al. (2022) – a lone crane foraging close to a water-body usually implied that its partner was nesting nearby. As Grey Crowned Cranes nest in areas that are difficult to access, we 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 nest-site approaching methodology detailed in Demmer et al. (2024) (Figure S1). Drone flights were kept to a minimum to decrease disturbance and lower the risk of nest or chick abandonment by parents. When monitoring families with chicks, the small size and cryptic colouring of Grey Crowned Crane hatchlings required closer and lower flights for accurate counts. During these flights, the pilot cautiously manoeuvred the drone, approaching the grouping at a diagonal angle, without hovering, to capture breeding metrics (spending approximately 20 seconds at the nest). Video recording was enabled throughout all approaches to facilitate post hoc recording of breeding metrics.

We considered a nest-site "active" if eggs were present or a crane was incubating on an identified nest (i.e. incubating; Figure 2B and D). Locations where courting pairs were observed without nests were revisited every two to three weeks. During each breeding site observation, we counted the number of eggs, hatchlings, juveniles, and fledglings and differentiated between these stages based on their size and plumage. Distinguishing juveniles from fledglings depended on whether chicks could fly (commonly takinge place 55–100 days after hatching; Gichuki 2000). Each nest-site was revisited at 2–3-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 from our analyses as missing the initial nesting stage results in biases towards identifying nest-sites that successfully hatch chicks (Jehle et al. 2004). Monitoring families after fledging was sometimes challenging due to the family's increased mobility. For this reason, we considered a breeding attempt successful when the offspring reached the juvenile stage. This usually included fledged chicks, but in other cases, families had moved off to join nearby flocks soon after chicks became more mobile, making it nearly impossible to identify specific families.

Breeding outcomes were measured in three ways: (1) total counts of offspring at each stage; (2) probability of offspring transitioning from one stage to another (total count in subsequent stage divided by total count in the previous stage); and (3) nest-site success when at least one juvenile or fledgling was observed.

Macro-environmental impacts

Daily rainfall data for the 2022/3 breeding season were sourced from local farmers known to keep accurate records by measuring millimetres of rainfall with standard 10 cm^2 circular rain gauges. These data were collected for each of the five regions where nest-sites were situated. We also collected macro-environmental data describing the broader patch and landscape-scale habitat type around each nest-site, further details of which are provided in Table 1.

We used GIS software to measure direct distances between each nest-site and important environmental descriptors (i.e. nearest building, road, agricultural land, and water-body) and to determine the dam and wetland surface areas (measured in m^2) (Table 1). The
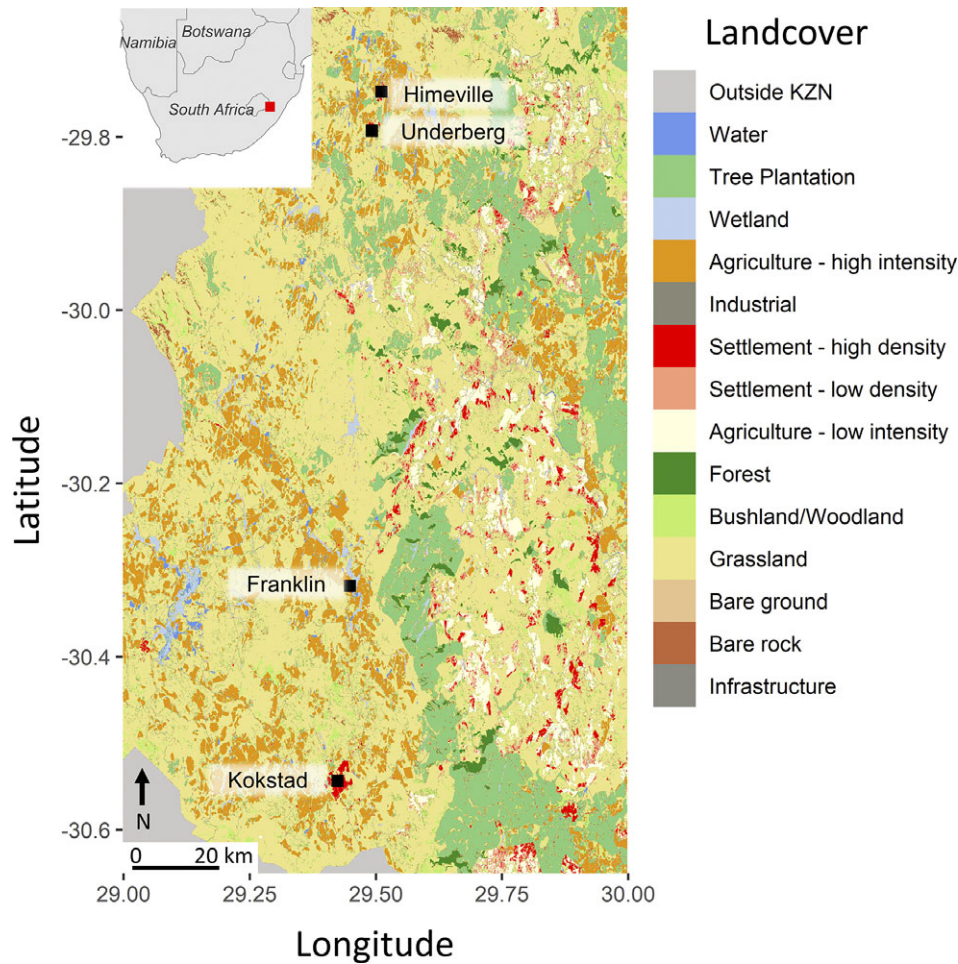
Figure 1. Distribution of the four main study sites within the southern Drakensberg, highlighting land-cover within surroundings. Specific nest-site locations have been omitted because this is potentially sensitive information and we do not have the landowner's permission to share this information publicly. Land-cover is based on a provincial land-cover map produced by the provincial conservation authority, Ezemvelo KwaZulu-Natal Wildlife (Ezemvelo KZN Wildlife 2008).

only categorical descriptor, vegetation height, was categorised through post hoc assessments using drone photographs taken within 1 m 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".

Statistical analyses

All statistical analyses were conducted in R version 4.3.1 (R Core Team 2022). To assess whether there was bias in our observations towards a particular study region, we compared the number of observations at each nest-site across regions with a Poisson generalised linear model (GLM) and a log link function.

General breeding outcomes

The date at which each developmental stage was most likely to be detected (an integer with 1 representing the first observation in the breeding season) was determined using a log-linear mixed effects model using the "lmer" function from the lme4 package (Bates et al. 2015). Developmental stage (eggs, hatchlings, juveniles, and fledglings), breeding outcome (success or failure), and the interaction of

these two factors as independent variables were included as fixed effects.

The number of offspring observed for a breeding attempt was assessed using a Poisson generalised linear mixed effects model (GLMM), implemented using the "glmer" function from the lme4 package, with developmental stage as the independent variable. Changes in the number of offspring over time (used to describe how and when stage transitions took place) were assessed with a generalised additive mixed model with a Poisson error distribution and a log link function, using the "gamm" function from the mgcv package (Wood 2011). Here, the number of offspring in each stage was allowed to vary as a function of days since nest-site detection. Since repeated observations took place at each nest-site throughout the breeding season, we controlled for this in all the above-mentioned mixed effects models by including a random intercept of the nest-site itself.

Transition probabilities

We used a binomial GLM with a logit link function to assess the probability of transitioning from one stage to the next. The transition types that we assessed were the three sequential transition types (eggs–hatchlings, hatchlings–juveniles, juveniles–fledglings), the egg-to-juvenile transition as a measure of nest-site success (the

Figure 2. Drone photographs depicting: (A) the view of a nest-site from afar; (B) a close-up of a Grey Crowned Crane *Balearica regulorum* nest-site; (C) a flooded nest-site; (D) incubating parent; (E) parents with two hatchlings and one egg at their nest-site; (F) parent foraging with juveniles.

chance that an egg will survive to a juvenile), and the chance of obtaining 100% success (whether all eggs would transition to juveniles). In a second model we assessed the change in transition probability of two transition types (eggs–hatchlings and hatchlings–juveniles) across a gradient of rainfall intensity using a binomial GLMM with a logit link function. We calculated rainfall intensity (mm/day) as the sum of the daily rainfall during each transition divided by the number of days the transition took to complete where higher values indicate greater rainfall over a shorter time period. Here, we included a random intercept of "region" to control for differences in total rainfall between the regions (Table S1). 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 across months ($F_{7,1236} = 340.34$, $P < 0.001$, Table S1), with greater rainfall intensity observed earlier in the breeding season. We controlled for this by incorporating a random slope effect of rainfall intensity within months to capture the variable rainfall intensity observed between the months. Juvenile fledgling transitions did not occur in all the regions and so this transition was excluded from this analysis. Unless otherwise stated, all results from these regression models are presented as means (± 95% confidence interval [CI]).

Macro-environmental impacts

We used a Principal Components Analysis (PCA) to explore trends in Grey Crowned Crane breeding outcomes across biophysical descriptors collected for each nest-site. Since 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, scaling each measurement between zero and one. We conducted the PCA using the "rda" function from the vegan package (Oksanen et al. 2022). We tested for the separation of centroids between successful and unsuccessful hatching (hatching success) and the production of juveniles (overall success) by implementing two analyses of variance, using Euclidean distance matrices, with the "adonis2" function in the vegan package. For both the

Table 1. Macro-environmental descriptors measured for each nest-site

Category	Unit	Description
Primary road (tar)	m	Distance to nearest tar road
Secondary (dirt)	m	Distance to nearest secondary road
Farm (dirt)	m	Distance to nearest farm road
Open water	m	Distance to nearest open water-body
River	m	Distance to nearest river
Wetland	m	Distance to nearest wetland edge (point at which vegetation changes from grassland to wetland type)
Natural grassland	m	Distance to nearest uncultivated grassland
Pasture	m	Distance to nearest cultivated pasture
Cropland	m	Distance to nearest cultivated cropland
Surface area	m^2	Surface area of nearest wetland or dam
Perimeter	m	Perimeter of nearest wetland or dam
Island	boolean	Whether the nest was on an island
Height	ordinal (1–5, short, short–medium, medium, medium–tall, tall)	Description of height of vegetation surrounding nest-site

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 or with the monitored family.

We identified the most important environmental descriptors using multi-model inference to complement the multivariate analyses. A binomial GLM including all main effects was fitted initially. Models with all possible combinations of predictor variables were then assessed using the "dredge" function from the MuMIn package (Bartoń 2023). From these we selected all models within two Akaike information criterion (AIC) units of the best-performing model (ΔAIC ≤2). To reduce the influence of potentially non-significant parameters included in these selected models, we applied a model averaging procedure, using the "model.avg" function from the MuMIn package to produce the final model (Arnold 2010).

There is a strong correlation between likelihood ratio tests and ΔAIC. A ΔAIC <2 (indicating that there is little evidence that models are significantly different) translates to P <0.157, approximating the 85% CI (Arnold 2010). As a result of this, we report both the 95% and 85% CIs in the final averaged model's presentation for these analyses (Arnold 2010; Sutherland et al. 2023). Effects significant at the 85% but not at the 95% level were referred to as "moderately significant".

Results

A total of 95 nests were identified and monitored across the five regions during the 2022/3 breeding season (Table S1). On average, each nest-site was observed 3.72 (3.44; 4.00) times, totalling 351 observations across all 95 nest-sites. The number of observations per nest-site did not differ between regions (χ^2 = 3.238, df = 4, P = 0.519; Table S1), indicating no monitoring bias between regions. Rainfall intensity did vary across regions, with Himeville recording the highest and Kokstad the lowest rainfall intensity respectively ($F_{4,1239}$ = 2.523, P = 0.039; Table S1).

The average dates where observations of the different stages were made are illustrated in Figure 3. 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).
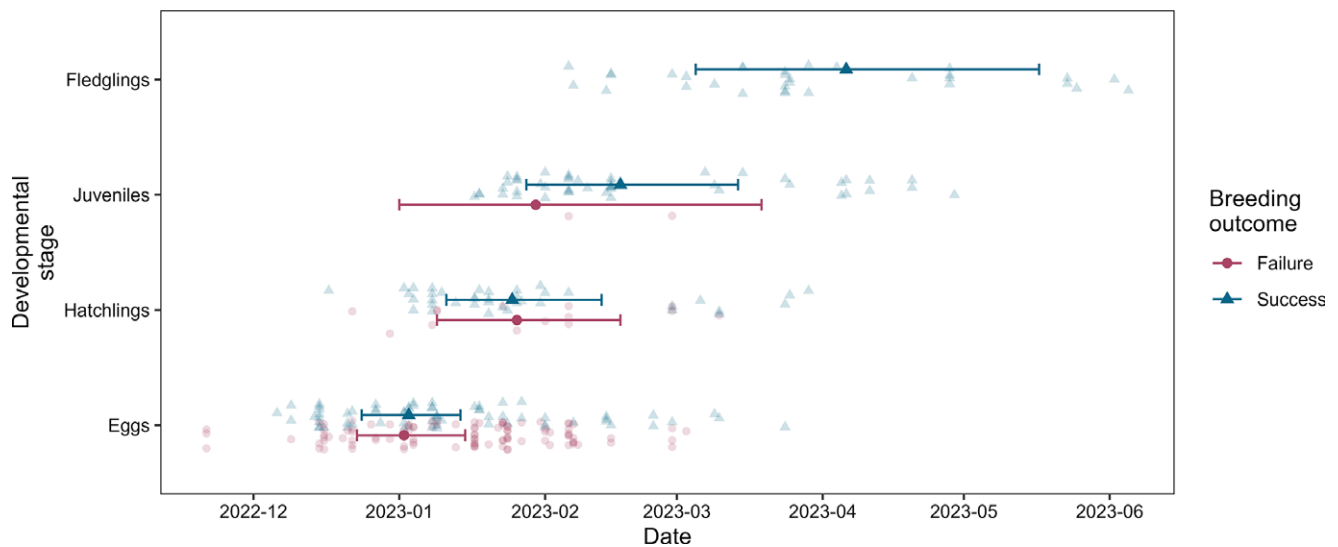
Figure 3. Mean (± 95% confidence interval) dates at which Grey Crowned Crane *Balearica regulorum* developmental stages were observed between successful and unsuccessful sites.
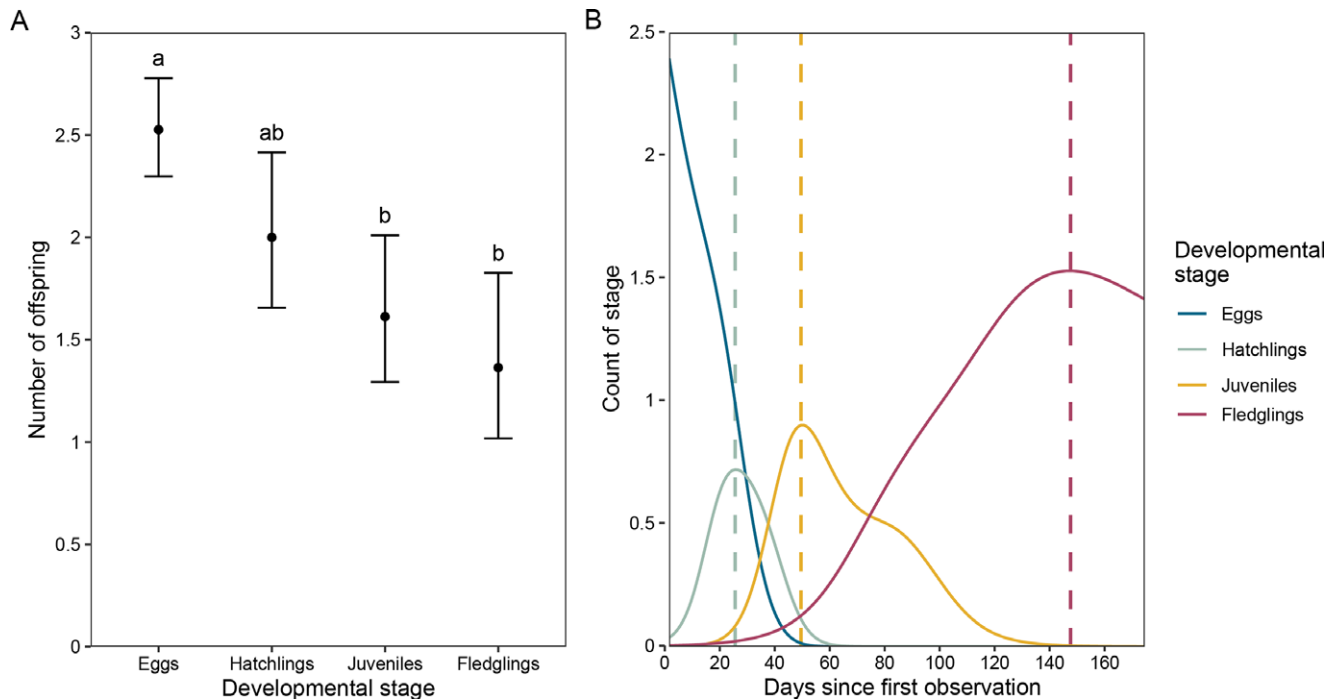
Figure 4. Counts of Grey Crowned Crane *Balearica regulorum* offspring at different developmental stages. (A) Error bars indicate 95% confidence interval, and shared letters indicate no evidence of significant differences. (B) Change in counts throughout the season. Dashed vertical lines indicate when the most offspring were detected for a developmental stage.

General breeding outcomes

The number of offspring per nest differed between developmental stages, with significantly more eggs recorded than juveniles or fledglings (χ^2 = 27.08, df = 3, P < 0.001; Figure 4A). 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 approximately 30 days of monitoring (estimated-df = 3.82, F = 70.69, P <0.001). Hatchlings (estimated-df = 3.95, F = 29.19, P <0.001), juveniles (estimated-df = 4.49, F = 23.26, P <0.001), and fledglings (estimated-df = 3.13, F = 35.32, P <0.001) all showed unimodal-type responses with peak counts occurring at 24, 48, and 146 days, respectively (Figure 4B).
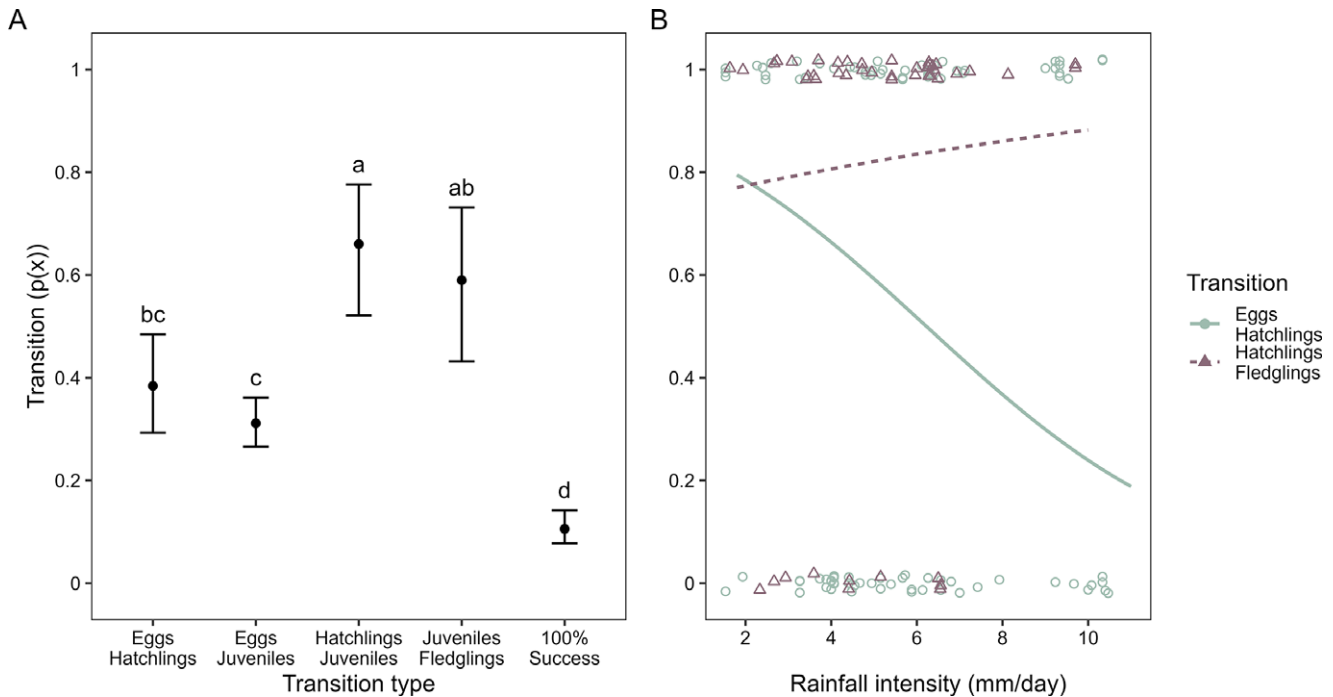
Transition probabilities

Grey Crowned Crane transition probabilities varied significantly among stage types (χ^2 = 30.73, df = 2, P <0.001; Figure 5A). No significant difference was found in the probability of transitioning from eggs to hatchlings (0.384 (0.293; 0.484)) in comparison to either transitioning from eggs to juveniles (0.311 (0.266; 0.361)) or transitioning from juveniles to fledglings. However, transitioning from eggs to hatchlings was less likely to occur than the transition from hatchlings to juveniles (0.660 (0.521; 0.776)), but the probability of transitioning from hatchlings to juveniles was not different from the probability of transitioning from juveniles to fledglings (0.590 (0.432; 0.731)). Transitioning from eggs to juveniles was less probable 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 – less than all other transition types considered. The probability of developing from eggs into

hatchlings was negatively affected by increased rainfall intensity (χ^2 = 4.071, df = 1, P = 0.044; Figure 5B), but transitioning from hatchlings to fledglings was not (χ^2 = 0.054, df = 1, P = 0.816; Figure 5B).

Macro-environmental impacts

The first principal component (PC1) explained 22.8% of the variation in nest locations (eigenvalue: 0.16). It included wetland areas (21.2%) and distances to buildings (16.0%), water edges (15.6%), tar roads (14.8%), and farm roads (13.3%) as the most closely related descriptors (Figure 6). The second principal component (PC2) explained 16.1% of the variation (eigenvalue: 0.11) and represented distances to natural grasslands (20.1%), buildings (15.7%), tar roads (14.8%), rivers (11.9%), and water edges (10.7%) (Figure 6). There were significant differences in the composition of nest-site metrics when considering hatching success (PERMANOVA, 999 permutations, pseudo-$F_{1,95}$ = 3.04, P = 0.006; Figure 6 – empty circles), but not in their overall success (PERMANOVA, 999 permutations, pseudo-$F_{1,95}$ = 1.86, P = 0.073; Figure 6 – filled circles). These separations occurred along PC1.

Multi-model inference identified 11 candidate models to explain hatching success and eight models to define overall breeding success. Model averaging procedures (Figure 7 and Table S2) revealed that hatching success decreased when nest-sites were further away from natural grasslands and buildings (at the 95% CI level) and when located at greater distances from dirt roads (at the 85% CI level). Considering overall success, nest-sites further away from buildings were less successful (at the 95% CI level), while reduced distance to natural grasslands and larger nearby dam surface areas were positively associated with increased breeding success (at the 85% CI level).

Figure 5. Transition probabilities (A) (mean ± 95% confidence interval) from one development stage to the next where (i) shared letters denote no difference, (ii) eggs–juveniles represents the probability that an egg was successfully reared, and (iii) 100% success indicates the probability that all eggs in a nest were raised successfully. (B) Across a rainfall intensity gradient (points are empty and jittered to show overlap).

Discussion

General breeding outcomes and transition probabilities

Grey Crowned Cranes lay some of the largest clutches in the crane family, with findings in Kenya reporting average clutch sizes of approximately 2.5 eggs (Wamiti et al. 2022), which aligns with our observations. Pomeroy (1980) observed larger crane clutch sizes at higher altitudes, possibly explaining our rare finding of four nests with more than three eggs (*n* eggs = 4) (Ivey and Dugger 2008; Sundar and Choudhury 2005). Other research reported that the reproductive success of cranes increases with stronger pair bonds, while frequent socialisation and having previously undertaken multiple breeding attempts also increases their reproductive success (Barwisch et al. 2022; Hammers et al. 2012; Ivey and Dugger 2008; Teitelbaum et al. 2017).

Unlike other crane species which frequently only invest in one hatchling (e.g. Wattled Cranes *Grus carunculata*), Grey Crowned Cranes attempt to raise all hatchlings (Morrison 2015; Morrison and Bothma 1998; Zelelew et al. 2019). Gichuki (1993) estimated an 83.6% hatching rate in Grey Crowned Cranes in Kenya, while Zelelew et al. (2019) reported a higher hatching rate (91.3%) in Black Crowned Cranes *Balearica pavonina* but inferred a low overall breeding success since less than half of the clutches in their study fledged. We observed substantially lower hatching rates than these studies, with only 38.4% of eggs hatching, 66.0% of hatchlings transitioning to juveniles, and 59.0% of juveniles surviving to the fledging stage. Multiplying these transition probabilities suggests a 14.95% chance that an egg will reach the fledging stage. These results support the earlier mentioned concerns of Assersohn et al. (2021) and suggests that Grey Crowned Crane breeding is most vulnerable during their nesting phase. After hatching, crane chicks remain vulnerable for another two to three months until they fledge. However, their survival probability usually increases thereafter, as they become older and

more adept at identifying danger and escaping predators themselves (Fox et al. 2019).

In our study, 10.6% of Grey Crowned Crane pairs managed to ensure that all eggs in their clutch transitioned to juveniles. The hatchling to juvenile/fledgling transition probability in Grey Crowned Cranes (one to two fledglings per pair) is higher than that of some other crane species. For example, Wattled Cranes are known to display low reproductive outputs, with the highest transition rate of hatchling to juvenile being recorded as 0.42 chicks per pair (in 1999, vs 0.66 for Grey Crowned Cranes) and approximately 0.25 chicks per pair in subsequent wetter years (Bento et al. 2007). Another comparison can be made with the Endangered Whooping Crane *Grus americana*, whose recovery is believed to be highly dependent on their ability to reproduce successfully (Butler et al. 2017). Yet, over eight years, Spalding et al. (2009) estimated a 30% hatching rate, with 47% of these Whooping Crane chicks surviving until the fledging stage – this translates to an overall breeding success of only 14%. Grey Crowned Cranes' general reproductive output throughout the duration of our study is comparable to that of Whooping Cranes (Spalding et al. 2009), which supports similar concerns about declining Grey Crowned Crane population trends.

Several studies have identified extreme weather events and human disturbances as major drivers of breeding failures among some Critically Endangered coastal and wetland ground-nesting birds (Ferreira et al. 2005; Powell et al. 2010; Smart et al. 2006; Spalding et al. 2009; Van De Pol et al. 2010). Therefore, in the sections that follow, we discuss how these climatic and landscape-level factors impact the reproductive outputs of Grey Crowned Cranes.

Macro-environmental impacts

Breeding birds incur high energetic costs when defending territories, incubating, and raising young (Gichuki 2000), but these costs
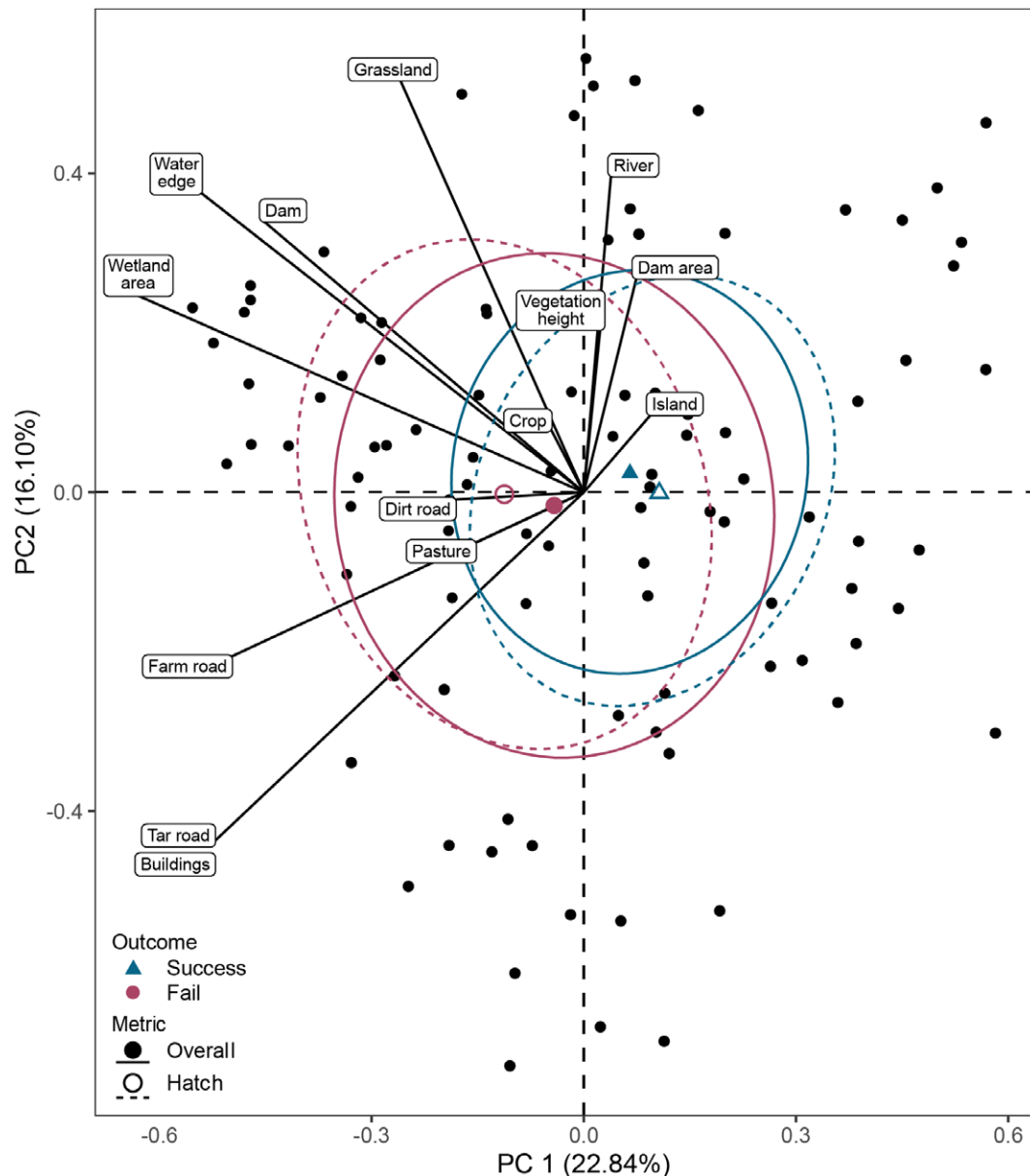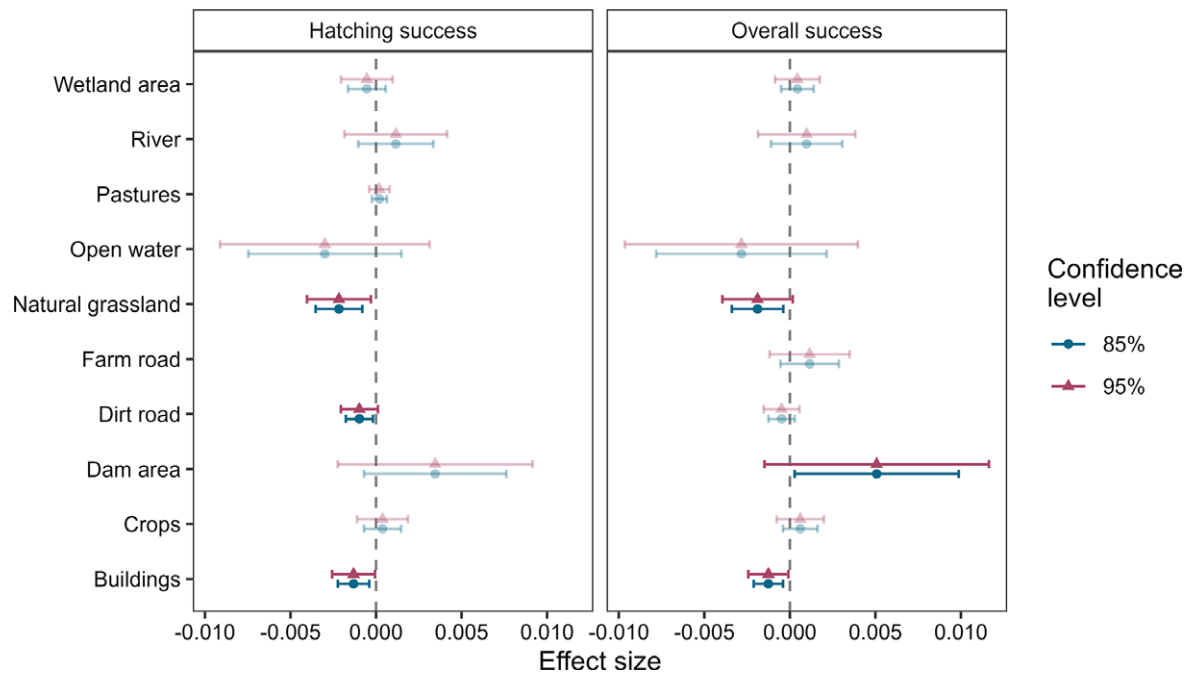
Figure 6. Grey Crowned Crane *Balearica regulorum* nest-sites and environmental descriptors along PC1 (eigenvalue = 0.16) and PC2 (eigenvalue = 0.11) of a Principal Components Analysis. Black points represent nest-sites, solid black lines are environmental descriptors. Envelopes represent the 95% confidence interval for the centroids (larger coloured points) of successful (blue) or failed (red) hatching (empty circle, dashed envelope) and overall breeding (filled circle, solid envelope) success. All descriptors are distances except for island (nest on island), vegetation height (height class around the nest-site), and areas (size of wetland or dam).

are escalated under suboptimal climatic conditions. It is noteworthy that our observations were made during a La Niña event, which resulted in unusually high rainfall; thus, the reported observations should be considered in this context. Whilst rainfall generally increases avian breeding success by optimising habitat requirements (Woolley et al. 2022), prolonged and heavy rain (especially over a short period) can lead to flooding or cooler weather and wet nest conditions, which may affect egg temperatures (Ivey and Dugger 2008). Maintaining egg temperature is crucial for species that share incubation duties between adults (including most crane species), as eggs are regularly exposed to the elements and predators during rotation (Du Rant et al. 2013; Ivey and Dugger 2008). Our findings showed that the egg phase was more vulnerable to intense rainfall than the hatchling and fledgling stages. Indeed, we observed nest abandonment by Grey Crowned

Cranes shortly after heavy rainfall and hail events (Demmer, personal observation), as has been reported for Sandhill Cranes *Grus canadensis* following rainfall events of >50 mm of rain within 24 hours (Fox et al. 2019; Nesbitt 1988).

Future climate predictions indicate more extreme events such as droughts and high rainfall in alternating years (Connell et al. 2021; Marcelino et al. 2020) and so the ability to adapt to a changing environment may influence the survival of a species (Charmantier and Gienapp 2014). Endangered bird species often exhibit reduced genetic variability, which can limit their ability to adapt to changing environmental conditions (Canteri et al. 2021; Evans and Sheldon 2008; Frankham 2005). This reduced adaptability may be particularly pronounced in non-migratory species like the Grey Crowned Crane, as they cannot easily relocate to more suitable habitats (Donnelly et al. 2022; Ramírez et al. 2018). Despite higher rainfall

Figure 7. Model averaged effect sizes of covariates on Grey Crowned Crane *Balearica regulorum* breeding success. Positive values indicate greater success with greater distance or area. Negative values indicate greater success with reduced distance (measured in metres) or area (measured in m²/1,000). Error bars indicate 95% (red) and 85% (blue) confidence intervals. Dashed vertical lines indicate no effect. Shaded values are non-significant at $P < 0.157$ (representative of ΔAIC = 2).

over the past season, we found no difference in breeding outcomes when breeding began earlier or later in the 2022/3 breeding season. However, since these observations are based on only a single breeding season, we encourage future studies to examine whether Grey Crowned Cranes show any changes in their breeding strategy between years of extreme and non-extreme climatic conditions.

Several observations of crane species attempting to renest within the same breeding season in an attempt to replenish lost broods have been reported (Nesbitt 1988; Thompson et al. 2022; Woolley et al. 2022). Renesting decisions depend on factors such as the time available to renest, environmental and parental condition, and the species' overall breeding strategy (Saalfeld et al. 2021). Whilst renesting can improve breeding success in some bird families (Hayes 2022; Ledwoń et al. 2023), it may not always be beneficial, as the long-term fitness of adults can decrease when energetic costs outweigh reproductive benefits (Jones et al. 1995; Swift et al. 2020). Some renesting attempts by Grey Crowned Cranes in our study ($n = 4$; excluded from analyses in this study) were successful, but others renested towards the end of the breeding season which may have resulted in a resource mismatch during the early stages of offspring development (Martay et al. 2023; Zelelew et al. 2019). Our small renesting sample size precluded analyses of renesting impact on overall reproductive output, but this could be explored in future studies.

Nest-sites were evidently vulnerable to flooding during high rainfall periods, which is likely exacerbated in agricultural landscapes due to wetland degradation and destruction. To effectively address the threat of breeding failures caused by habitat loss and degradation, future conservation strategies and management interventions should focus on protecting habitats that are important to the entire life cycle of Grey Crowned Cranes. Restoring degraded wetlands for example, will not only increase biodiversity and food availability, but could also mitigate severe water level changes during periods of intense rainfall. Responsible land-use practices

and wetland buffer zones are vital tools in wetland restoration, but they must be implemented in a way that supports and informs landowners to ensure their cooperation (Jepthas and Swanepoel 2019; Wood 1999). Further protection from flooding may also take the form of artificial nesting platforms in suitably vegetated areas, since Grey Crowned Cranes readily nest in man-made water-bodies (Chuyu et al. 2022).

Human disturbances and anthropogenic landscapes

Cranes are generally sensitive to human disturbances (Coverdale 2006; Ivey and Dugger 2008; Végvári et al. 2011; Wang et al. 2011), but in South Africa, cranes occur primarily outside of protected areas. While this increases their vulnerability to human pressures and unmanaged changes in their environment (Olupot et al. 2010), Hemminger et al. (2022) reported that several crane species, including the Grey Crowned Crane, benefit from readily available food supplies resulting from crop residues. An unfortunate drawback of this is that cranes may cause crop damage, with Grey Crowned Cranes observed affecting up to 4.1% of maize plants (van Niekerk 2018). Losses caused by insects are comparably higher (10–16%) (Bradshaw et al. 2016; Oerke 2006; Raphela and Pillay 2021). However, both crane and insect-related crop damage can be substantially reduced by planting seeds treated with insecticide, which reduces crane-related crop damage to just 0.23% (van Niekerk 2018). The residual effects of consuming pesticide-treated seed in small amounts is largely unknown, and this, together with other studies on the impact of Grey Crowned Cranes on agricultural activities, should be explored further.

Several alternative, but highly effective, approaches exist to deter cranes from agricultural lands (Austin and Sundar 2018). These methods include changing the timing of crop planting to avoid overlap with crane presence, selecting less preferred crops when cranes are present in high numbers, planting marginal lands as

"diversionary fields" to distract cranes away from the principal croplands, providing supplementary feeding, and applying responsible seed treatments to deter birds (Austin and Sundar 2018). Each of these methods can be applied regardless of the scale of agricultural activity being undertaken. Despite the benefits of increased foraging opportunities, intensive agricultural practices (e.g. grazing, cropping, and damming; Dalu et al. 2017) drastically transform natural ecosystems, modifying sensitive breeding habitats (Bartzen et al. 2010; Sica et al. 2018). Nesting closer to human disturbances during vulnerable and energetically taxing breeding stages (e.g. incubation) may also lower breeding success (Seress et al. 2020). This is supported by observations of the migratory White-naped Cranes *Grus vipio*, which have shifted their nest-sites further away from roads and settlements (Wu et al. 2014).

The physical nest-site location directly or indirectly influences breeding success or failure (Nalwanga et al. 2004; Wu et al. 2014). For example, nesting on islands is common in several waterbird species (e.g. Burgess and Hirons 1992; Scarton and Valle 2020) and was also observed to promote positive breeding outcomes in our study – likely through a decreased risk of predation by terrestrial mesopredators. Grey Crowned Cranes 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 our study were surrounded by tall vegetation, likely to conceal nest-sites from terrestrial predators (Olupot 2016). Yet, our results indicated that vegetation height did not necessarily promote reproductive success. This may be explained by nest-sites still being visible to aerial predators despite tall vegetation. Indeed, we observed three instances when birds of prey were feeding on exposed eggs at nests (Figure S2). Considering the simplicity of earlier recommendations, we suggest that new dam sites consider incorporating these features into their planning to offset potential losses to pre-existing breeding habitats due to wetland flooding or degradation. Furthermore, our observations revealed that nearly all nests were situated in dense bulrushes (*Typha capensis*). Therefore, both new and existing dam sites should aim to encourage the establishment of this species to promote the suitability of nesting sites around the dam.

Although our study did not assess predator presence around nest-sites, predation via natural predators is an on-going challenge for ground-nesting birds that inhabit farmland landscapes (Bravo et al. 2023). We observed and received reports from landowners of some predatory incidences on Grey Crowned Cranes during this study ($n = 6$; Demmer, personal observation) by generalist mesopredators (i.e. serval *Leptailurus serval* and jackal *Lupulella mesomelas*). These types of predators are commonly associated with intensively managed pastures during calving and lambing seasons (Humphries et al. 2016; Skead 1979) and are known predators of ground-nesting birds (Beja et al. 2014), and we presume that mesopredator density would be lower in natural grasslands and near buildings during this time. We therefore speculate that this could account for some of the observed positive associations between Grey Crowned Crane reproductive success and the closer proximity of their nesting to natural grasslands and buildings. Interestingly, our findings suggest that nesting closer to secondary roads and buildings (an indicator of human presence) is associated with increased hatching success in Grey Crowned Cranes, suggesting a tolerance to (if not a preference for) some human disturbances (Archibald et al. 2020; Wamiti et al. 2022). One potential explanation for this is that mesopredators typically avoid regions where humans are present (Reilly et al. 2022) which, in turn, benefits nesting Grey Crowned Cranes. Alternatively, Fox

et al. (2019) suggest that such relationships between birds and nesting location may be in response to decreased suitable breeding habitats, forcing cranes to choose nest-sites in suboptimal locations (e.g. Miller and Barzen 2016).

Finally, nest-sites situated in water-bodies with larger surface areas improved overall breeding success – perhaps because large, healthy water-bodies act as biodiversity hotspots, meeting a greater number of habitat requirements for significant life events of inhabiting species (Creed et al. 2017; Donnelly et al. 2022; Toussaint et al. 2021). These larger water-bodies may also be able to buffer flooding instances better than smaller water-bodies, especially given the greater flood attenuation ability of highland wetlands (like those in our study) compared with lower altitude wetlands (Åhlén et al. 2022; Wu et al. 2023).

Conclusions

Our study provided key insights into the breeding outcomes of Grey Crowned Cranes in unprotected areas and identifies macro-environmental factors that influence their reproductive success or failure. We observed significant attrition from egg to hatchling stages, which increased with higher rainfall intensity. Successful breeding outcomes were higher when Grey Crowned Cranes nested near buildings and natural grassland vegetation, suggesting some adaptability to human disturbances. However, the benefits of nesting near agricultural areas may be short-lived if wetland vegetation becomes degraded, reducing future nesting sites. We recommend refining monitoring methods and implementing more frequent, detailed, and long-term monitoring of Grey Crowned Crane breeding to gain a better understanding of this species' long-term breeding success. Insights from long-term monitoring will undoubtedly assist with maintaining wetland ecosystem health and ensure continued breeding opportunities for this Endangered species.

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