Blue Crane hatching success in the Overberg: assessing the influence of land-use class, temperature, and incubation behaviour

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Table of contents

Abstract

The Overberg region of South Africa holds the largest remaining population of Blue Cranes globally. The area is an agricultural landscape, with a mosaic of pasture and cereal-crop fields that mimic the Blue Crane's natural grassland habitat. This landscape served as a replacement for the now largely transformed Grassland Biome of South Africa, which historically housed most of the country's Blue Cranes. Recently, the steadily growing Overberg population of Blue Cranes is showing signs of a changing population trajectory, which may indicate the start of a population decline. This study aims to explore changes in hatching success as a potential mechanism behind changes in the Overberg Blue Crane population trajectory. I explore how hatching success of Overberg Blue Cranes has changed in the last two decades by comparing hatching success in the breeding seasons of 2021/22 and 2022/23 with that recorded in a previous study in 2003/4. Additionally, I consider the influence of two major global change drivers: land-use and climate change, on the hatching success of eggs in this population. I found no change in the current hatching success of Overberg Blue Cranes compared to 2003/4, which suggests that a change in population trajectory is likely due to factors other than hatching success. I also found no significant difference in the hatching success of nests in cereal-crop fields vs those in pastures. This is at variance with the results of the 2004 study, which documented lower hatching success of cereal- crop nests. Mean maximum daily air temperature was included in my top model for hatching success and had a significant negative effect on hatching success, even though air temperatures remained relatively low (did not exceed 30°C) during my study. I therefore suggest that managers should prioritise further studies on the impact of temperature on hatching success, given that rising temperatures associated with climate change may result in an overall reduction in hatching success in this and other Blue Crane populations over time. Additionally, incubation behaviour, summarised according to the proportion of time eggs are left unattended during incubation, was not correlated with air temperature or land-use class but was significantly correlated with hatching success, such that eggs left unattended for a greater proportion of time were more likely to fail. This suggests that incubation disturbance, perhaps due to human activity in the agricultural landscape, could reduce the hatching success of Blue Cranes in the Overberg. These findings will help direct future studies and raise awareness regarding sustainable practises for farmers in the area as we aim to conserve this Blue Crane population now, and into the changing future.

1. Introduction

Currently, two of the most important drivers of global change are land-use change and climate change (Thuiller et al., 2008). Together, climate and land-cover are powerful predictors of whether a habitat can support a population of any given species. Changes in either can impair an individual's ability to reproduce or find shelter or food, and alter population dynamics (Thuiller et al., 2008; Sohl, 2014). Consequently, climate and land cover trends can be used to predict where populations will occur, and whether they will persist (Pressey et al., 2007; Matthews et al., 2011; Sohl, 2014). Drivers of global change such as land use and climate change can cause populations to struggle where they once flourished, or vice versa (Thuiller et al., 2008; Sohl, 2014). If we can understand the mechanisms through which these drivers impact populations, we will have a better understanding of how we can proactively intervene to offset the negative impacts of global change (Cabeza & Moilanen, 2001; Pressey et al., 2007).

Many studies predicting future shifts in distributions or population dynamics assume that climate change is the greatest driver of these shifts (Sinclair et al., 2010; Barbet-Massin et al., 2012; Jongsomjit et al., 2013; Watling et al., 2013). They assume that each species has a range of climatic variables it can physiologically tolerate, which generally remain unchanged (Sinclair et al., 2010). This "climatic envelope" is used to predict how climate change might impact populations (Sinclair et al., 2010). Indeed, many models based on climatic variables can accurately predict current distributions (Thuiller et al., 2004; Sinclair et al., 2010; Jimenez-Valverde et al., 2011; Bucklin et al., 2014). This suggests that climate-driven models can extrapolate population persistence in response to climate change (Araujo et al., 2011). This is useful for focusing conservation efforts on areas likely to house population strongholds in the future, as global temperatures rise, and extreme weather events increase in frequency (IPCC-43, 2016). However, focusing on climate change neglects the influence of other drivers of global change, such as land-use change. Climate-only models assume that climate drives land cover, but this neglects land cover change resulting from anthropogenic land-uses, which are often independent of climate (Sinclair et al., 2010). This is a massive oversight, considering that, between 1960 and 2019, global land use change impacted around a third of the earth's land surface (Winkler et al., 2021). Therefore, wherever possible, land use and land cover variables should be considered in addition to climatic variables (Sohl, 2014). Barbet-Massin et al. (2012), for example, found that species distribution models significantly increased in accuracy when they accounted for both climate and land use and land cover variables, vs a climate-only approach. This result is widely supported by the literature (Matthews et al., 2011; Jongsomjit et al., 2013; Watling et al., 2013; Riordan & Rundel, 2014).

The impact of land use change on land cover is particularly important in heavily human-modified landscapes, such as agricultural areas. Agriculture is commonly viewed in opposition to conservation because it generally decreases biodiversity in comparison to natural habitat (O'Connor & Shrubb, 1986; Wright et al., 2012). This is particularly true today, since technological advances and increased demand have led to the intensification and homogenization of agriculture (Sala et al. 2000; Donald et al., 2001; Loh 2002; MEA 2005). However, for certain species, particularly open-habitat savannah, or grassland species (which describes around a quarter of globally threatened and near-threatened bird species, for example, Denham's Bustards (*Neotis denhami*), Grey Crowned Cranes (*Balearica regulorum*) and Secretarybirds (*Sagittarius serpentarius*) (IUCN, 2022)), agricultural landscapes can provide a substitute for dwindling natural habitat (Wright et al., 2012). Some open-habitat species now depend on cultivated areas where pastures or crops have replaced unsuitable, dense vegetation with open fields. Wright et al. (2012) found that 28% of threatened and near-threatened bird species rely on artificial terrestrial landscapes, most of which are agriculture. In Africa, this figure is around 33% (Wright et al., 2012). This highlights how conservationists should consider agriculture not only in terms of reducing its impact on natural habitats, but also managing established farmlands to help protect agriculture-dependent wildlife (Mas & Dietsch, 2004). Species differ in their requirements for cultivated landscapes. Some require low-intensity farming practises, or heterogenous mosaics to persist, whereas others can tolerate high-intensity, monoculture farming (Fuller et al., 2004). Therefore, changes in farming approaches and land use can alter the suitability of a region for previously established populations (Wright et al., 2012).

The Blue Crane *(Anthropoides paradiseus)* is an excellent case study for the influence of land-use change and possibly climate change on population dynamics. The species is largely endemic to South Africa, with a small sub-population in Namibia (Allan, 2005). Historically, most individuals resided in the eastern grasslands of South Africa, where open plains probably supported over 100000 individuals (Allan, 2005; Pettifor et al., 2009). However, the grassland biome in South Africa has been extensively transformed due to its productive soils and flat topography, resulting in large-scale biodiversity loss. Today, the grassland biome is considered critically endangered in South Africa (Reyers et al., 2001; McCann et al., 2007). Consequently, by the 1970s the total Blue Crane population in South Africa was reduced to 50000 individuals, a declining trend that continued and worsened into the 1980s (Archibald & Meine, 1996; Allan, 1997; Shaw, 2015). Those two decades saw an estimated 90% population decline of Blue Cranes in the eastern grassland biome of South Africa (Johnson & Barnes, 1986; Tarboton, 1992; Allan, 1997; McCann, 2001). Since the 1980s, all populations of Blue Crane outside of the Western Cape have continued to decline (Shaw, 2003). Today, an estimated 20000 – 25000 Blue Cranes remain in South Africa (Beilfuss et al., 2007; McCann et al., 2007) and the species was listed as both Globally and Regionally Vulnerable since 2000 (McCann, 2000; BirdLife International, 2022). In 2015, updated population assessments of core Blue Crane populations in South Africa found that, on average, the regional population has recovered enough to now be listed as Regionally Near Threatened (Shaw 2015) though the global species status remains as Vulnerable (Shaw, 2015; BirdLife International, 2022).

Of the remaining individuals, an estimated 50% inhabit the agricultural areas of the Western Cape (McCann et al., 2007; Pettifor et al., 2009). Blue Cranes favour open habitats with short vegetation and maximum visibility to allow for early threat detection (Morrison & Bothma, 1998; McCann et al., 2007; Bidwell, 2004). Historically, the agricultural areas of the Western Cape housed Renosterveld and Fynbos vegetation types which were too tall and dense for Blue Cranes to forage and breed in (Shaw, 2003; McCann et al., 2007; Pettifor et al., 2009). This habitat was replaced with a mosaic of grazing pastures and cereal crops such as wheat and barley that mimic a natural grassland structure (Allan, 1997; Shaw, 2003; McCannn et al., 2007; Pettifor et al., 2009). This transformation provided suitable foraging and nesting habitat for cranes, with few natural predators (Shaw, 2003; Hofmeyr 2012, van Velden, 2017). When Blue Cranes first colonised the Western Cape, the population grew slowly, with only 600 individuals counted in the early 1980s (Siegfried, 1985). What followed was a rapid population increase to more recent estimates of around 12000 individuals (Pettifor et al., 2009; Hofmeyr, 2012).

Recently, there have been signs that the Blue Crane population growth in the Overberg is tapering and possibly entering a decline (Young & Harrison, 2020; Christie Craig, unpubl. data). While Young and Harrison (2020) attributed recent reductions in summer Blue Crane count data to the population entering a state of dynamic equilibrium, more recent analyses comparing the same count data to population estimates put forth by Hofmeyr (2012), found a 22% decline in the Overberg population between 2011 and 2019 (Christie Craig, unpubl. data). If this population has indeed entered a declining phase, this would suggest that the area has become less suitable for Blue Crane survival and reproduction. This makes it important to proactively identify any regional changes responsible for reduced habitat suitability. Two possible changes worth investigating include the aforementioned main drivers of global change: land-use change, and climate change.

Almost all Blue Cranes breeding in the Western Cape nest in agricultural fields (Pettifor et al., 2009). Grazing pastures and post-harvest cereal crop fields are particularly favoured, and these are also the dominant land cover classes in the Overberg (Bidwell, 2004; Pettifor et al., 2009; Hofmeyr, 2012). A study by Bidwell (2004) investigated which landscape factors determined nest site selection and how, in turn, site selection impacted hatching success. Bidwell (2004) estimated a crude population hatching success rate of approximately 57% and hatching success was also found to vary significantly according to the land-use class of the nest field, with pasture-nesters experiencing higher success than cereal-crop nesters (Bidwell, 2004). The region’s dominant cereal crops are wheat and barley, which farmers harvest during the crane’s breeding season (Allan, 2005; Stead, 2021). Post-harvest, stubble fields provide suitable nesting habitat whereas prior to harvest, only grazing pastures are available to breeding cranes (Bidwell, 2004; Pettifor et al., 2009). This means that early breeding pairs disproportionately nest in pastures (Bidwell, 2004; Pettifor et al., 2009), which suggests that Bidwell’s (2004) finding that pasture-nesters experienced a greater hatching success compared to cereal-crop nesters likely reflects the well-established trend that early-season breeders are more successful (Perrins, 1970; Verhulst & Nilsson, 2007). However, regardless of the effect of land-use class on hatching success, this Blue Crane population relies on the region’s dominant land use types and the crops’ seasonal cycles. These factors depend on what farmers choose to do with their land and may change if other, more profitable options arise due to shifts in demand or climate (Altwegg & Anderson, 2009; Pettifor et al., 2009; van Velden et al., 2016; Davis, 2018). This places the Overberg Blue Crane population in a potentially vulnerable position.

Additionally, climate change may be a driver of land-use change in the region. The Western Cape is predicted to become hotter (Midgley, 2005) with an average maximum summer temperature increase of 1.5–3°C and an average minimum summer temperature increase of 1–3°C by 2060 (CSAG, 2014). Inland regions are less moderated by the cooling effect of the ocean and will likely see more extreme temperature increases than coastal areas. Winter rainfall is also projected to decrease (Midgley, 2005; CSAG, 2014) and rainfall patterns will become less predictable in terms of amount and timing (Midgley, 2005). These climatic changes may reduce the suitability of the region for the current crops, which may pressure farmers to shift from cereal crops, to crops less dependent on predictable rainfall, and perhaps less suitable for Blue Cranes (Fairbanks, 2004; Altwegg & Anderson, 2009; Pettifor et al., 2009; Davis, 2018).

Blue Cranes are also directly threatened by climate change. Morrison (1998) demonstrated that Blue Cranes’ breeding success is dependent on spring and summer rainfall patterns. Indeed, the timing of rain influences the timing of cereal harvests, which can only take place when the crop is below a certain moisture point (Shamsollah et al., 2020). Unpredictable, unseasonal rainfall can result in late harvests, and delay breeding for cranes nesting in cereal fields. Blue Cranes nest in the summer, in exposed nest sites on the ground (Allan, 2005). This exposes them to both incoming solar radiation and thermal radiation reflected off the surrounding ground, which places incubating adults under high heat loads (Albright et al., 2010). As high temperatures increase in frequency and duration due to climate change, so too will the costs associated with incubation (McKechnie & Wolf, 2019). High temperatures may force incubating adults to trade-off self-preserving behaviours such as water- or shade-seeking, against continued incubation, which helps to protect developing embryos from lethal temperatures, potentially at a great physiological cost to the adult (Oswald & Arnold, 2012; Martin et al. 2018; DuRant et al., 2019). If adults are forced to abandon incubation at high air temperatures, this may result in reproductive failure. Alternatively, even if high temperatures do not influence adult incubation behaviour, adults may still leave eggs exposed for foraging purposes, during incubation changeover, i.e., adults switching incubation shifts, or when adults are flushed from the nests by predators or human activity (McGowan & Weston et al., 2011; DuRant et al., 2019). If the adults do not account for high temperatures during off-bouts by reducing incubation recess duration where possible, embryonic development and survival may be impacted (Walsberg & Voss-Roberts, 1983; Webb, 1987; DuRant et al., 2013).

This study investigates whether the recent decline in Blue Crane numbers in the Overberg could be linked to a change in their hatching success and potential factors influencing hatching success. More specifically, I aim to understand 1) how hatching success has changed in the Overberg Blue Crane population over the last two decades, and 2) if and how current land-use, daily air temperatures and adult incubation behaviour impact hatching success. The first aim is a comparative analysis of the hatching success of Blue Cranes in the Overberg over two successive summers (2021/22 and 2022/23) vs 2003/04 data reported by Bidwell (2004). Almost two decades later, my study repeats some of the methods of Bidwell (2004), to determine if hatching success has changed in the intervening years. I predict that hatching success has declined since 2004, and that this may have played a role in the recent Blue Crane summer count data in the Overberg (Young & Harrison, 2020). My second aim investigates how, taken together, land-use class and air temperature, as well as adult incubation behaviour influence the hatching success of Overberg Blue Cranes. I predict that pasture-nesters will have a higher hatching success than cereal-crop nesters, in line with Bidwell's (2004) findings. I also predict that high daily air temperatures will increase the amount of time incubating adults spend off the nest, which might reduce hatching success. Hopefully, my findings will contribute towards understanding how and where to direct future studies and conservation efforts.

2. Methods

Study site

The Overberg municipality in the Western Cape, South Africa, is characterised by low-lying plains, frequently intercepted by hills and mountains (Barnes, 1998). The geology of the region is dominated by the Malmsbury and Bokkeveld rock groups, which break down to form soils high in clay and silt (Low & Rebelo, 1996). The area is dominated by agriculture, where it was once dominated by Fynbos and Renosterveld vegetation types of the Clape Floristic Region. Now, only 0.5% of the original natural vegetation of the region remains untransformed (Rebelo et al., 2006; Topp & Loos, 2019; Young and Harrison, 2020). Most low-lying regions are rotated between grazing pastures for livestock, and crops, including wheat and canola, with some fruit orchards scattered throughout (Conradie et al., 2009, van Velden et al., 2016).

The Overberg has a Mediterranean climate, with cool, wet winters, and hot, dry summers (van Velden et al., 2016; Stead, 2021). Total annual precipitation is 450–600 mm, with a peak in July (van Velden et al., 2016; Dippenaar, 2022). This study took place near the town of Caledon (Figure 1), where summer temperatures peak in February, with a mean maximum temperature of 29.2°C (Dippenaar, 2022). Monthly mean maximum temperatures from September–January, the Blue Crane breeding season, range between 20.2°C and 29.0°C, and rainfall between 16.1 and 34.1 mm (Dippenaar, 2022).

Data collection

Nest location

Nests were located by driving the same farm roads every day, scanning for Blue Crane pairs. My line of sight was largely determined by the topography of the land, though generally I could spot cranes within 2 km of the road with the help of binoculars. When I spotted cranes in the distance, I would stop and watch them through binoculars to assess whether they were displaying courtship behaviours or behaviours indicative of an active nest (e.g., jumping, flapping their wings, and chasing one another, territorial calling as a pair, or sitting on the ground, possibly on eggs). I drove daily both the route north of Caledon (50 km) and southeast of Caledon during my search (30 km; Figure 1). I also requested local residents to report any courting and/or incubating cranes on local social media groups. Once I had located multiple active nests, I alternated daily between the northern and south-eastern loops in search of new nests.

When I repeatedly spotted the same pair in the same field, I would watch them from the vehicle to search for a nest site. When I encountered a sitting crane, I would continue observing it until it stood, and I could scan the ground beneath it for the presence of eggs. If eggs were present, I would try to discern clutch size using binoculars, or, if the nest site was too far, I would slowly approach the nest until the crane moved away and I could confirm clutch size. If there was only one egg, I left and returned two days later, to allow for a second egg to be laid (Allan, 2005). Once I confirmed two eggs in the nest (or verified a clutch size of one, i.e., no second egg laid after two days) I entered the nest field, and slowly approached the nest until the adult cranes moved away. Once the eggs were exposed, I tried to reach them as quickly as possible to measure them and set up the nest for observations (see below), so that my approach took no longer than a few minutes. I never spent more than 15 min at a nest site and left the area for a minimum of 2 hr after a nest visit to allow the cranes to return to the nest undisturbed. After at least 2 hr, I returned and parked at least 500 m from the nest and used binoculars to verify that the cranes had resumed incubation. Measurements and nest setup for data collection were as follows.

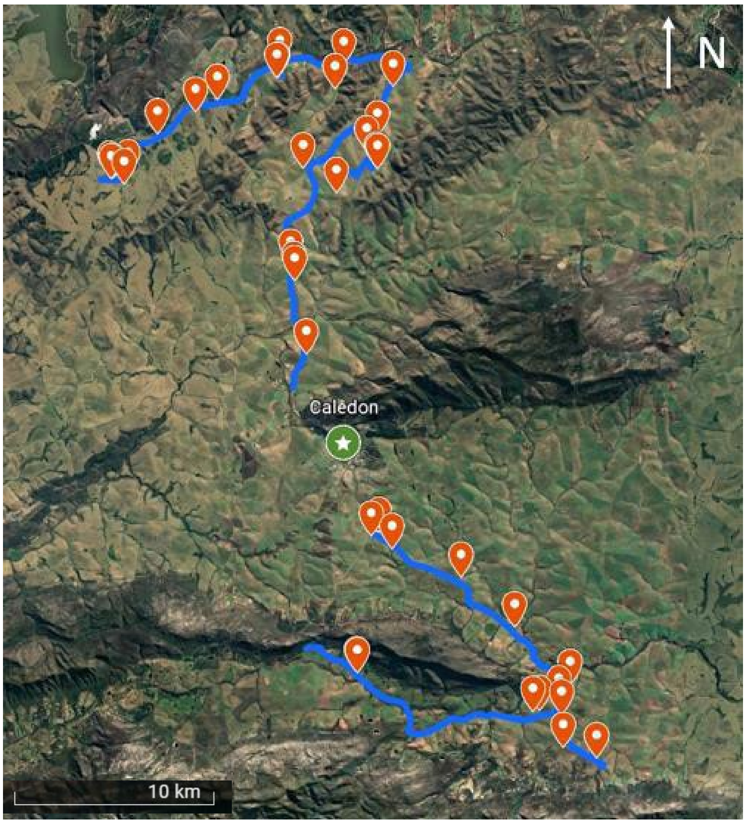

Figure 1. The locations of all 39 Overberg Blue Crane nests included in this study (red place-markers), relative to the town of Caledon, indicated by a green star. Road transects are indicated in blue, and include the route driven to the north of Caledon (50 km) and the south-east of Caledon (30 km).

Nest setup

Egg measurements

Once I reached the nest, I took the waypoint and noted clutch size. I then used Vernier callipers to measure the length, maximum breadth, and breadth at 90° of the maximum breadth of each egg to the nearest mm. These measurements were used to calculate egg volume, calculated as length *maximum breadth *breadth@ 90°of maximum breadth, as per Bidwell (2004). I then separately weighed each egg to the nearest 0.1 g using an Ohaus pan scale.

Camera trap setup

At each nest, I set up a south-facing camera trap 5 m north of the nest, orientated to prevent sunlight distorting the image. As the ground was generally too hard to hammer a stake into, I cable-tied cameras to a wooden stand, constructed with a wide base, which I weighed down with stones. I used a combination of Spartan (Model SR2-BK) (Frontier Pursuits Technology, Minnesota) and Cuddeback Professional Colour (Model 1347) (Non-Typical Inc., Wisconsin) camera traps. Each was initially set to take a picture and a 10 sec video between the hours of 6:00 and 18:00, whenever the camera was triggered by motion. However, the motion trigger setting proved unreliable, so in my second field season, I additionally set the camera to take one picture every minute from 6:00 to 18:00. I chose to only set up my cameras to capture diurnal incubation behaviours as both night and day data capture would more quickly drain camera batteries and fill up SD cards. This would require shorter intervals between nest visits and increased disturbance of incubation. Given that my study was aimed at investigating the impact of climate change, the influence of high daily temperatures was most relevant, which justified the lack of nighttime camera triggers which would lack paired focal data and increase the risk of incubation abandonment as these cameras had white light flash.

Land-use class

I classified each nest field according to the dominant land-use class, into one of five classes: cereal crop, dryland pasture, fallow (ploughed), natural, and non-cereal stubble crop (e.g., canola, for which the post-harvest stubble is taller and more coarse than cereal crops, and generally avoided by nesting cranes (Bidwell, 2004; Christie Craig, pers. com).

Weather data

Weather data were sourced from the Elsenberg Agricultural Research Institute, University of Stellenbosch. They have multiple weather stations in the area, and the data are publicly available at https://gis.elsenburg.com/apps/wsp/#. I used weather data from a weather station (Model Stratus 2000) (iLeaf, Hortec Weather Services) in Caledon, at the centre of my study area, that was installed in 2020. The weather station collects air temperature data at 5 min intervals. For each nest, I considered air temperatures from the date of my first nest setup, until the date a nest failed or hatched.

Behavioural focals and camera trap footage analysis

In 2021, I carried out a maximum of eight 1.5 hr focal observations at each nest. When possible, I conducted four focal observations between day 1 and day 12 ('early incubation') and a second four between day 12 and day 24 of incubation ('late incubation'). Two focals were conducted in the morning (8:00–11:30) and two during the heat of the day (12:00–15:30). To minimise disturbance, focals were never performed on the same day I visited the nest to weigh eggs, and I tried to schedule them over a range of daily temperature maxima per nest (e.g., one heat of the day focal on a cool day (< 25°C) one on a hot day (>25°C)). In 2022, I increased focal duration to three hours so that I could observe multiple changeover events per nest to better estimate changeover frequency and duration of incubation recesses (i.e., when eggs were left unattended by both parents). Consequently, I reduced the total number of focals per nest to four in total, with one behavioural observation during the heat of the day, and one in the morning between day 1 and 10 and between day 10 and 20 of incubation. I changed the length of the time blocks representing early and late incubation periods in my second season because I discovered eggs had often hatched before day 24 (likely due to my inability to accurately determine lay dates at nests I found with clutches already complete).

Data collected during focals included: the time the incubating adult spent sitting on the nest versus standing over it (shading), when an incubation changeover occurred, and whenever eggs were left exposed ('incubation recesses'). When the eggs were left exposed, I noted the reason if obvious e.g., flushed by a farm worker/vehicle, which I classified as "human" disturbance, or flushed by cows or sheep, which I classified as "livestock" disturbance. I also noted where the crane went e.g., remained in field, or flew out of sight, and how long the eggs remained exposed. Additionally, during each focal, I noted any obvious heat dissipation behaviours e.g., wing drooping, gular fluttering, shade seeking, or water drinking. I also observed daily footage and pictures from each camera trap, between the hours of 8:00–16:00 (so that my camera-trap and focal data were collected within an easily comparable time window) and noted the same behaviours as above (excluding why the incubating crane left, and where it went, as the footage did not capture this).

Hatching success was summarised as follows: every nest that hatched at least one chick was considered a "success" and assigned a value of 1. Those that hatched no chicks were labelled a "failure" and assigned a value of 0. At failed nests, where there is footage showing eggs suddenly disappearing between consecutive photos or clips, or appearing damaged, the nest was considered "predated" even if there is no footage of the actual predation event. Nests where there is footage of the incubating adults leaving behind intact eggs, and not returning were considered "abandoned." Two nests that were abandoned immediately after I visited the nest were considered "chased" and distinct from nests that were seemingly abandoned for reasons unrelated to my presence (these latter abandonments occurred at varying time periods post nest set up). A nest for which I had footage of a combine harvester driving over the eggs was assigned "combine harvester" as the cause of failure. Finally, a nest failure was "unknown" if the eggs disappeared and there was no footage to conclusively identify if predation, or another factor, was the ultimate cause of nest abandonment by the adults.

Statistical Analyses

Preliminary analysis of summer Blue Crane count data

There are conflicting interpretations of the Blue Crane summer CAR count data presented in Young & Harrison (2020). Recent, unpublished analyses (Christie Craig, unpubl. data) on the same count data indicate that the population is in decline, rather than in a state of dynamic equilibrium as concluded by Young & Harrison (2020). Because I cannot cite an analysis yet to be published, I performed my own very simple preliminary analysis on these Blue Crane summer CAR count data (for data collection methods see Young & Harrison, 2020). This was conducted as a means of investigating whether recent population trends seem to indicate a decline, which was not the conclusion of Young & Harrison's (2020) analysis. I conducted a simple break-point analysis, using the segmented package (Muggeo, 2003) in R (R Core Team, 2022). I used a Davie's test (Davies, 1987) to assess whether a significant breakpoint (i.e., change in trend) existed in the data, then fitted general linear models with Gaussian error distribution to subsets of the data below and above the breakpoint to assess trends in crane numbers through time. Examination of model residuals suggested that models with Gaussian error distribution fitted these data better than models with Poisson distribution, despite the fact these are count data.

Hatching success comparison 2003/4 vs 2021–2022

I calculated the crude hatching success as the number of nests hatching at least one egg per the total number of nests *100 (Bidwell, 2004). I then compared my output to Bidwell's (2004) using a Fischer's exact test (Fischer, 1922). Additionally, for each nest that failed, I plotted the inferred reason for the failure. I did not compare my nest failure data to that of Bidwell's (2004) as we used different methods to infer the reason behind nest failure.

Correlate of hatching success

My aim was to assess the importance of land-use class (cereal-crop, pasture, other), air temperature variables (mean maximum air temperature, T_{max}; mean minimum air temperature, T_{min}; air temperature variance, T_{var}), and/or parental behaviour (i.e., proportion of time eggs were left unattended) in predicting hatching success (0 = fail, 1 = at least one egg hatched successfully); controlling for the possible influence of clutch quality (i.e., egg size and clutch size) and lay date (Julian date, with 01/10/21 and 01/10/22 set as day 1 for each respective field season), as both are known to correlate with hatching success in other species (Perrins, 1970; Moreno et al., 1991; Heaney & Monaghan, 1995; Monaghan & Nager, 1997; Both, 2010).

I had incomplete datasets for incubation behaviour from both focals and nest cameras, due to fieldwork constraints and camera trap malfunctions. To create as complete as possible a dataset for the proportion of time eggs were left unattended, I therefore summarised both focal data and video footage data according to the mean proportion of time incubating adults were simultaneously off the nest, leaving the eggs exposed (pfocal and pvid respectively). I tested for a correlation using Pearson's product-moment correlation test in R (Freedman et al., 2007), between the mean proportion of time nests were left unattended in my focal data, to that measured in my video data. The two variables were significantly correlated ($r = 3.24$, p-value < 0.05). This allowed me to create a new calibrated variable ("p(off)"), that estimated the mean proportion of time adults left nests unattended in the missing video data, using existing focal data. This was achieved using the equation $y = mx + c$, with y = the new calibrated variable, m = the model estimate for the correlation between pfocal and pvid, x = proportion of time eggs were left unattended in the video data, and c = the intercept term estimate of the model.

I used the information theoretic approach known as Akaike's Information Criterion, corrected for a small sample size (Sugiura, 1978), hereafter referred to as "AICc," to compare a set of biologically meaningful candidate models containing subsets of the key variables land-use class, Tmax, Tmin, Tvar, p(off), egg size, clutch size and Julian date, to determine which best explain patterns of variation in hatching success (Symonds & Moussalli, 2011).

To determine the final model set of candidate models to compare using the AICc approach, I first assessed the relationship between each variable and hatching success, to investigate the relative influence of each on the response variable. This allowed me to select the subset of variables most suitable for fitting biologically meaningful candidate models to my data (Hockey et al., 2011). However, clutch size had a particularly significant effect on hatching success, because all four single-egg clutches failed. As a result, clutch size resulted in quasi-complete separation, which impacted the model selection process (Webb et al., 2004), so I removed clutch size as a variable of interest. Model AICc values were similar for simple models of hatching success as a function of each temperature variable alone, so I included all three temperature variables when building candidate models.

Finally, I assessed correlations between all variables, to ensure that correlated variables were not fitted within the same model, as per Fox & Monette (1992). Initially, I predicted that the mechanism linking high temperature to Blue Crane nest failure would be due to changes in the incubation behaviour of the adults, as they balance incubation requirements with their own thermoregulatory needs. I therefore tested the relationship between p(off) and each of the three temperature variables in turn, using linear models with Gaussian error distribution. I log-transformed the p(off) variable to satisfy the assumption of normality of residuals. I found no effect of any of the temperature variables on p(off). This meant that I could include p(off) and temperature variables within the same candidate model sets for hatching success.

As the temperature variables were correlated with one another and were similarly supported by model AICc comparisons during data exploration, I included each in separate models. Julian date was correlated with mean maximum and mean minimum air temperatures, and also with land-use class, so I did not include this in the candidate models as land-use class and air temperature were included in my core variables of interest. Lay date is hypothesised to affect nest success through correlations with parental quality: inclusion of egg size and parental care behaviour might capture these effects. My final candidate model set included 17 models, including the null model for comparison (Table 1). Models were fitted as binomial general linear models with nest success as my response variable (1 = hatched, 0 = failed). The candidate model selection process was conducted using the AICcmodavg package in R (Mazerolle 2020). Models with lower AICc values were considered stronger models than those with higher AICc values, and any models with a delta AICc value > 2 from the top model, with the lowest AICc value, were considered unsupported (Symonds & Moussalli, 2011).

Additional analyses

Finally, to further explore the influence of the three variables comprising my top model on hatching success, I considered hatching success in terms of "nest outcome" which considered successful nests against nest failures, with the latter further broken down into the main reason behind each failure including "abandoned" (n = 4 nests) and "predated" (n = 6 nests), and the remaining reasons behind nest failures (n = 2 nests) combined into the failure reason "other." I then considered each of the three variables that were included in the top model of hatching success; egg mean volume (egg size), mean maximum temperature (Tmax) and mean proportion of time eggs were left unattended during incubation (p(off)) (log-transformed to achieve normality in the residuals) as the response variable in three respective linear models with gaussian error distribution, each with nest outcome as the predictor variable.

All data are presented as means ± 1 standard error and p-values < 0.05 are considered statistically significant. Model fits were checked by plotting histograms of residuals and I tested for zero-inflation of binomial models using the DHARMa package in R (Hartig, 2022).

3. Results

Preliminary analysis of summer Blue Crane count data

The output of my preliminary, breakpoint analysis of yearly summer Overberg Blue Crane count data is summarised in Figure 2.

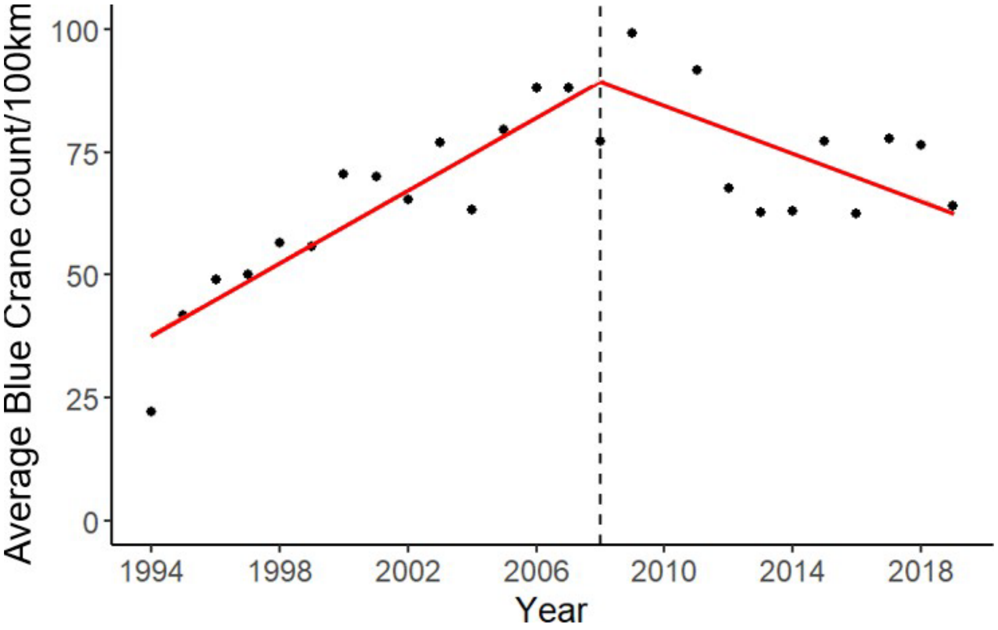

Figure 2. The average summer count of Blue Cranes per 100 km in the Overberg, between the year 1994 and 2019, including fitted trendlines before and after the breakpoint year, indicated by the dashed line (2008).

There was a significant breakpoint in the CAR count data (1994–2019) at the end of 2008 (est = 2008.72 ± 1.18, p-value < 0.05). From 1994–2008, Overberg summer Blue Crane counts indicate an increasing population trend (est = 3.69 ± 0.47, t-value = 7.92, p-value < 0.05). However, this trend changes after 2008, after which the count data indicate a declining population trend (est = -2.89 ± 1.16, t-value = -2.50, p-value < 0.05) (Figure 2).

Crude hatching success

My analysis of the 2021–2022 crude hatching success result compared to that calculated in 2004 by Bidwell (2004) found no significant difference between the crude hatching success rates of the two studies (Bidwell = crude hatching success of 57%, Bouwer = crude hatching success of 68%) (odds ratio est = 0.71, p-value = 0.40).

I monitored nest outcomes at 39 nests, of which 25 hatched and 12 failed. Of the 12 failed nests, six were predated and four were abandoned. At two nests, adults did not return after I placed the camera trap, so I assumed these were abandoned due to research activities (i.e., nest visits and camera trap placement) and I considered them as "chased." At one nest, the eggs were crushed by a combine harvester and at another, the reason behind the nest failure could not be determined. The two "chased" nests were excluded from subsequent analyses, as they were influenced by the study process itself, and not the variables of interest.

Model selection

The variety of candidate models considered and their respective AICc and delta AICc values are summarised below (Table 1).

Table 1. The model selection values considered when selecting the best-supported binomial general linear model for the influence of land-use class, temperature, and adult incubation behaviour, on the hatching success of Blue Cranes in the Overberg, including the model predictor variables(s), the number of model parameters (k), the model information score (AICc), the difference in AIC relative to the best-supported model (delta AICc), and the relative predictive power of the model (AICcWt). Models are ordered from smallest–largest AICc values and the single top model with delta AICc < 2 is in bold. Variables considered were the mean maximum (Tmax) and minimum (Tmin) air temperatures, as well as the air temperature variance (Tvar) (all three in °C), mean egg volume (egg size, mm^3) and the proportion of time adults spent off the nest during incubation (p(off)). n = 37 nests.

model predictor variable(s)	k	AICc	delta AICc	AICcWt
Tmax + p(off) + egg size	**4**	**33.53**	**0.00**	**0.53**
Tvar + p(off) + egg size	4	36.92	3.39	0.10
p(off) + egg size	3	37.13	3.60	0.09
Null	1	38.12	4.59	0.05
Tmin + p(off) + egg size	4	38.46	4.92	0.05
Tmax + egg size	3	38.52	4.99	0.04
Tmax + p(off) + land-use class + egg size	6	38.53	5.00	0.04
Egg size	2	39.83	6.30	0.02
Tvar + p(off) + land-use class + egg size	6	40.23	6.70	0.02
Tvar + egg size	3	40.33	6.80	0.02
P(off) + land-use class + egg size	5	40.82	7.29	0.01
Tmin + egg size	3	41.45	7.92	0.01
Tmax + land-use class + egg size	5	42.79	9.26	0.01
Land-use class + egg size	4	42.83	9.30	0.01
Tmin + p(off) + land-use class + egg size	6	43.03	9.50	0.00
Tvar + land-use class + egg size	5	43.78	10.25	0.00
Tmin+ land-use class + egg size	5	45.11	11.58	0.00

The best model for predicting hatching success was the model including the mean maximum air temperature (Tmax), the proportion of time adults spent off the nest during incubation (p(off)), and the mean egg volume (egg size) (model outputs shown in Table 2) (Table 1). The next best-supported model, consisting of air temperature variance (Tvar), the proportion of time adults spent off the nest during incubation (p(off)) and the mean egg volume (egg size) was > 2.00 delta AICc points below the top model (Table 1). There was little evidence that land-use class was important in predicting hatching success: the model with lowest AICc including land-use class was 5 AICc points away from the top model.

Table 2. Model outputs from the top model predicting hatching success, including predictors mean maximum air temperature "Tmax", the proportion of time adults left eggs unattended during incubation "p(off)" and "egg size". Reported values include the estimate, standard error, z- and p-values for each variable and the intercept. Significant effects ($p < 0.05$) in bold. Model is a generalised linear model with binomial error distribution. n = 37 nests.

variable	**estimate**	**standard error**	**z-value**	**p-value**
intercept	***3.30e***	***1.56e***	***2.115***	***0.03***
p(off)	**-2.53e**	**1.07e**	**-2.35**	**0.02**
Tmax	**$-9.58e^{-1}$**	**$4.74e^{-1}$**	**-2.02**	**0.04**
egg size	$-1.74e^{-5}$	$1.96e^{-5}$	-0.89	0.37

The influence of incubation behaviour and temperature on hatching success

Hatching success was significantly negatively associated with both the proportion of time parents left the eggs unattended (p(off)) (z-value = -2.35, p = 0.02; Table 2, Figure 3a) and the mean maximum air temperature (Tmax) (z-value = -2.02, p = 0.04; Table 2, Figure 3b). However, there was a non-significant relationship between hatching success and egg size (z-value = -0.89, p = 0.37; Table 2).

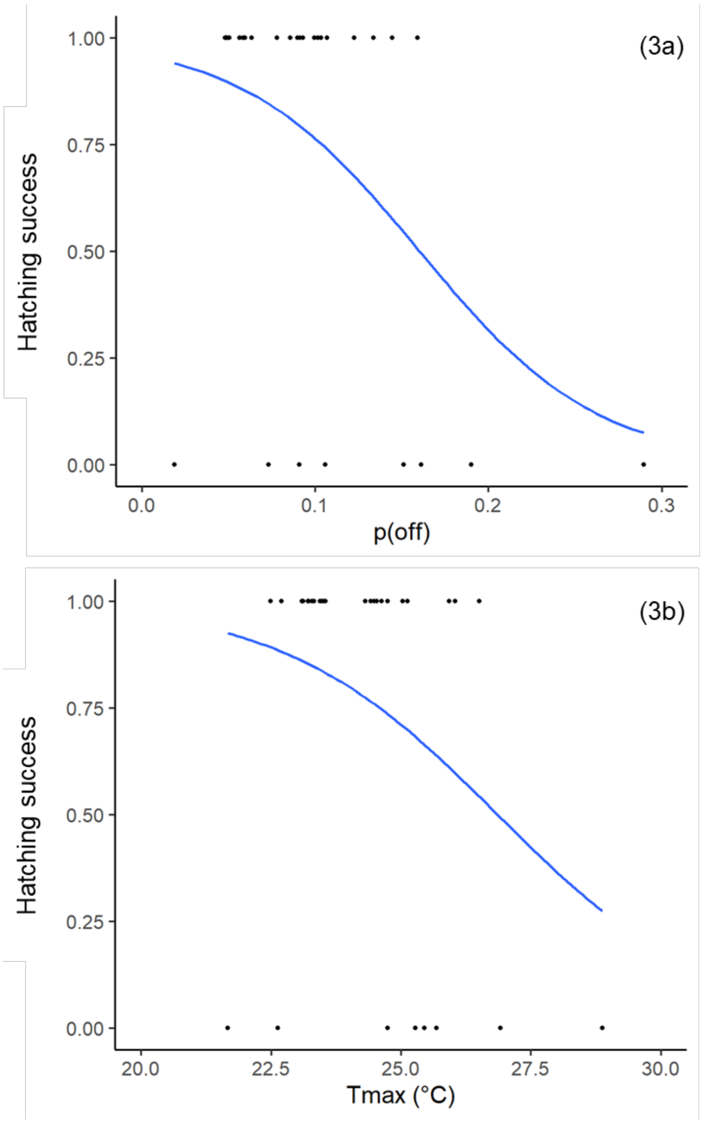

Figure 3. Blue Crane hatching success in the Overberg as a function of the proportion of time adults spend off the nest during incubation (p(off), 3a) and mean maximum air temperature during incubation (Tmax (°C), 3b). n = 37 nests.

Additional effects

Finally, the relationship of mean egg volume (egg size), mean maximum temperature (Tmax), and the proportion of time eggs were left unattended during incubation p(off), with nest outcome is summarised in the following figure (Figure 4).

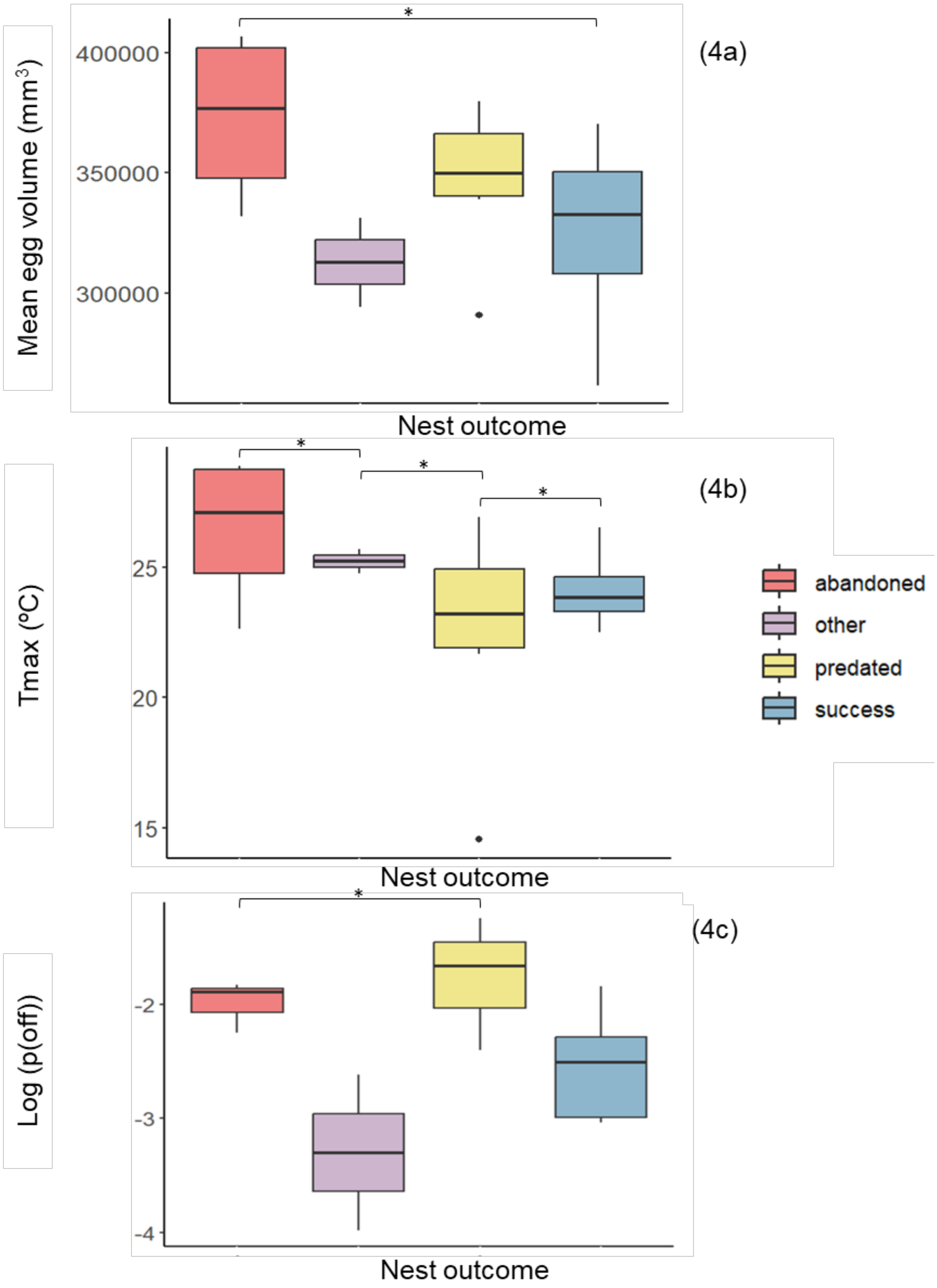

Figure 4. The relationship between nest outcome of Overberg Blue Cranes and the three variables included in my top model of nest success: mean egg volume (egg size, mm^3, Figure 4a), mean maximum temperature (Tmax, °C, Figure 4b) and the proportion of time adults were off the nest during incubation (p(off), Figure 4c). Nest outcome is broken into reasons behind nest failure including: nests where adults left their eggs never to return (abandoned, n = 4 nests), nests that were predated (predated, n = 6 nests) and nests that failed due to a combine harvester (n = 1 nest) and for unknown reasons (n = 1 nest), these latter two were combined into a single category (other, n = 2 nests). The final nest outcome category is

for successful nests (n = 25 nests). Significant differences in the variables considered between nest outcome categories is indicated with a star. Total n = 37 nests .

Abandoned nests had significantly larger eggs than those of nests that succeeded (t-value = 2.74; df = 33; p < 0.05). However, there are no significant relationships between abandoned nests and nests that failed for different reasons (namely, predated and “other” nest failures) (Figure 4a). Abandoned eggs experienced significantly higher temperatures that nests that failed for other reason (abandoned vs other: t-value = 3.30; df = 28; p < 0.05) (Figure 4b). In turn, eggs that failed due to other reasons experienced significantly lower temperatures than nests that were predated (other vs predated: t-value = -3.86; df = 28; p < 0.05) (Figure 4b). Additionally, predated eggs experienced higher temperatures than successful nests (predated vs successful: t-value 3.00; df = 28; p < 0.05) (Figure 4b). Adults incubating at nests that were predated spent a greater proportion of time off the eggs than those incubating abandoned nests (abandoned vs predated: t-value = 2.90; df = 33; p-value < 0.05) (Figure 4c). There were no other significant relationships between the proportion of time adults spent incubating nests and nest outcome (Figure 4c).

3. Discussion

In this study, I provide an updated crude hatching success estimate for the Overberg Blue Cranes for the first time since 2004. Hatching success has not significantly changed, which suggests that future studies investigating the potentially declining trajectory of this population should focus on other aspects of fitness such as juvenile or adult survival rates. Additionally, I found no significant effect of land-use class, namely, cereal crop and pasture, on hatching success. This means future land-use changes in favour of either pasture or cereal-crop land-use classes should potentially exert little effect on Overberg Blue Crane hatching success. Future studies should consider other potential land-use change decisions facing regional farmers, and how these might impact on the population. Higher mean maximum air temperatures were significantly negatively correlated with hatching success. This is a particularly noteworthy result, considering that air temperatures recorded in this study never exceeded 30°C, and suggests that higher regional temperatures due to climate change may increasingly affect hatching success in the future, which may eventually result in a significant decline in hatching success over time. It is therefore imperative that this relationship between air temperature and hatching success continue to be monitored. Interestingly, incubation behaviour was not correlated with air temperature, though it did have a significant effect on hatching success, with adults off the nest for a greater proportion of the incubation period hatching fewer chicks than more attentive parents. This means that eggs are vulnerable when they are left unattended during incubation, and there is a risk that farmers or farm workers will flush cranes as they work. Farmers, therefore, need to be made aware of this so they can try to keep their distance from active nests during the breeding season as we attempt to conserve this vital Blue Crane population.

Blue Crane numbers in the Overberg appear to have stabilised since about 2010 (Young & Harrison, 2020), with some indications of population decline over approximately the last decade (Christie Craig, unpubl. data) (Figure 2). Despite this, my data do not indicate reduced Blue Crane hatching success in 2021 and 2022 relative to Bidwell's 2004 estimate (Bidwell 2004). Therefore, it seems unlikely that the recent change in the Overberg Blue Crane population trajectory is related to reduced hatching success. Instead, declines could be due to reduced breeding attempts in adults, or negative trends in other phases of reproduction. For example, a recent study comparing the mean fledgling number per nest across four key Blue Crane populations in South Africa found that Overberg and adjacent Swartland (monthly nest checks, 2018–2022; Endangered Wildlife Trust, unpub. data) breeding pairs successfully fledged significantly fewer chicks than the eastern grassland and Karoo populations (monthly nest checks, 2008–2013; Endangered Wildlife Trust, unpub. data). Therefore, high mortality rates between hatching and fledging may be contributing to reduced reproductive success of Overberg Blue Cranes. Alternatively, some factors could be reducing adult survival in the region: the other factor of the fitness equation. A study by van Velden et al. (2016) found a relatively low adult survival rate (0.72) for Overberg and Swartland Blue Crane populations relative to an earlier study conducted on the Karoo Blue Crane population (0.96) (Altwegg & Anderson, 2009). The van Velden et al. (2016) study concluded that this estimate was not in line with the projected increasing population trends at the time, or previous knowledge on the life-history traits of this species. They therefore attributed this low survival estimate to tag loss throughout the mark-recapture process (van Velden et al., 2016). Perhaps now, it is time to revisit adult survival estimates in the region, given the current signs of a population decline and the local abundance of threats to adult Blue Crane survival such as powerlines and wind turbines (Davis, 2018). Finally, emigration may be responsible for the recent population trajectory shift, though this seems unlikely. van Velden et al. (2016) investigated the movement patterns of Overberg Blue Cranes, and found that, on average, adults remained within 25km of their natal site (van Veldon et al., 2016), with only around 4% of individuals spotted in the Overberg resighted in the near-by Swartland population. That said, it remains important to consider changes in movement and dispersal behaviour in the future.

Bidwell (2004) was able to find 70 nests in the Overberg region in one year, while I only found 39 nests over the course of two breeding seasons (2021 and 2022) in the same area. If we assume a similar search effort in each of the two studies, this suggests that Blue Crane breeding pair densities could be lower than they were approximately two decades ago. However, it is difficult to compare search efforts between the two studies. I searched for nesting pairs on all but two of the farms noted in Bidwell (2004), and six additional farms that Bidwell did not consider. I also had the benefit of technology that Bidwell (2004) did not, in the form of local farmer WhatsApp groups. This allowed me to communicate with farmers directly, which may have increased my search effort compared to the 2004 study. Conversely, however, only a handful of farmers consistently communicated with me, and I received only a few invitations to explore farms unrestricted. My sense is that the farmers are more concerned with security than they were in 2004, due to a real or perceived uptick in crime since then (Clack & Minaar, 2018). Many farmers have tracking collars on their sheep, that notify the farmer when their herds run (Thys Delport, local farmer, pers. com). This meant that many farmers wanted a warning before I visited a nest, to confirm that I was chasing sheep, and not stock thieves. This added security restricted my driving transect largely to public-access dirt roads, which may have reduced my search effort relative to the 2004 study. What we do know from Bidwell's (2004) study, however, is that Blue Cranes do not select nest sites relative to dirt roads, which suggests that, if Bidwell (2004) and I drove similar distances, there should not be marked differences in search effort despite differences in farm access. My conclusion here is that while the differences in samples sizes in 2004 vs 2021/22 over roughly the same area might indicate lower crane population density since 2004, it is difficult to ascertain the relative search effort deployed in each study, due to changes in land access and technology. Regardless of the cause, however, my sample size was low relative to Bidwell's (2004), which suggests that future studies on breeding Blue Cranes in the Overberg should divide search efforts between multiple researchers or make use of satellite or drone technology to cover a larger area to attain larger sample sizes for increased confidence in results.

Relationships between land-use class and hatching success

While it is encouraging that hatching success has remained constant between my study and Bidwell's 2003/4 study (Bidwell 2004), it is important to investigate whether this status quo could be threatened by climate change and/or landscape change driven by the land-use decisions of farmers. In my study, land-use class had no influence on hatching success as indicated by its absence from the best-supported model of hatching success. Indeed, models containing land-use class were less well-supported than the null model in my analysis (Table 1). This contrasts with Bidwell (2004) who found that cereal-crop nesters were significantly less successful than pasture-nesters. There are a variety of potential explanations for this different result. The most obvious of these is my small sample size compared to Bidwell (2004). The number of cereal-crop nests I found was particularly low (n= 13) which makes it difficult to detect significant impacts of land-use, if present. During my first field season, there was an unseasonal amount of rain in the Overberg. This delayed cereal-crop harvest, because farmers had to wait for the crops to dry before commencing harvest, which delayed the 2021 harvest until mid-late November, far later than normal (Thys Delport, local farmer, pers. comm). I therefore only collected data for two cereal-crop nests in 2021, reducing my overall cereal-crop sample size. Unfortunately, Bidwell's raw datasets have been lost, and he does not mention his sample sizes of nests in cereal-crop vs pasture-fields, only the relative hatching success of each. Additionally, Bidwell (2004) combined the same five land-use types considered in both of our studies into "biologically sensible" classes to meet the necessary assumption of a chi-square test, but he does not elaborate on how exactly he did so. In my study, most of my nests were either in cereal or pasture fields, with only four nests of 39 in other land-use classes. I therefore combined these four into an "other" land-use class for my analysis. It is, therefore unclear if our respective findings concerning the effect of land-use class on hatching success are comparable, given that our land-use classes may be comprised differently.

Relationships between air temperature and hatching success

A crucial finding of my study is the significant ($p < 0.05$) negative relationship between mean maximum air temperature and hatching success (Figure 3b). The heat load experienced by eggs is moderated by the incubating parent, but on hot days the eggs of ground-nesting birds can heat rapidly when parents leave the nest (Mougeot et al., 2014; Carrol et al., 2015). I therefore predicted that high maximum air temperatures would reduce hatching success in Blue Cranes on the basis that while developing avian embryos do require high temperatures for successful development (32.00–35.00°C) (Webb 1987; Williams 1996) most species have a maximum temperature threshold, above which high temperatures become detrimental and even lethal, rather than beneficial (Bourne Walsberg & Voss-Roberts, 1983; Webb, 1987; DuRant et al., 2013). We do not know what this upper limit is for Blue Cranes, but a study investigating the optimal incubation temperature of captive-bred Whooping Crane (*Grus americana*) eggs found that egg temperatures exceeding 33.64°C were associated with reduced hatching success (Edwards et al., 2021). My study explored the influence of air temperature on hatching success; however, air temperature is only one of the factors determining the heat load placed on developing embryos. Other key factors not considered here include measures of convection and radiation, as well as the radiative heat transfer capacity between the eggs with their environment, which is itself determined by the structural features of the egg, and the nest site (Dzialowski, 2005). It would be interesting, and more accurate, to further explore these interacting factors in subsequent studies, using species-calibrated operative temperature models (Dzialowski, 2005). However, given that the Blue Crane is a Vulnerable, TOPS classified species in South Africa (NEMBA, 2004), this poses challenges regarding obtaining a Blue Crane egg for modelling purposes and/or replacing a viable egg with an egg model in an active nest.

Despite these limitations, air temperature may correlate with the range of operative temperatures in the environment and indeed, has been shown to correlate with fitness and hatching success in numerous other bird species (McKechnie et al., 2012; Smit & McKechnie, 2015; Wada et al., 2015; Clauser & McRae, 2017; Bourne et al., 2019; Bourne, 2020; Conradie et al., 2020; Sharpe et al., 2021). The effect of air temperature on hatching success is usually mediated through incubation behaviour, with higher air temperatures resulting in longer off-bouts during the incubation period, or nest abandonment (Bueno-Enciso et al., 2017; Clauser & McRae, 2017; Bourne, 2020; Sharpe et al., 2019). However, I did not find a significant correlation between air temperature and the proportion of time incubating Blue Crane adults left their nests unattended. This is a puzzling result which suggests that other factors are influencing incubation recess behaviour to an extent which might mask any air temperature-related effects. Given that Blue Cranes nest in agricultural fields, these factors likely include human or animal disturbances, which in turn result in the exposure of eggs to high heat loads influenced by ground and solar radiation, that allow us to glimpse the potential impact of high temperatures on hatching success.

My finding that mean maximum air temperature exerted a significant negative effect on hatching success during the study period may have important conservation implications for the Overberg Blue Crane population, and indeed the whole species. The result is particularly noteworthy when one considers that mean maximum air temperatures during the study period did not exceed 30°C, relatively modest temperatures at which to observe such an effect. A study on Southern Pied Babblers *Turdoides bicolor* (Bourne et al., 2020), for example, found reduced hatching success only at air temperatures exceeding 35°C. This discrepancy could be due to higher operative environmental temperatures on the ground in the sun (e.g., at Blue Crane nests) vs other nest sites in the landscape (e.g., the shaded sites in trees where Southern Pied Babblers nest) at similar air temperatures (Carrol et al., 2015). This emphasizes the need for species-specific investigations into the relationship between air temperature and operative egg temperature in Blue Crane nests. Nonetheless, the comparatively low tolerance of Blue Crane eggs to high air temperatures is alarming and suggests a need for comparative studies to confirm this finding. This study was conducted over relatively cool and wet summer months, so continued monitoring of the relationship between mean maximum air temperature and hatching success in this population would be helpful to understand how the relationship presents under a variety of breeding season conditions. Alternatively, comparative studies could explore the apparent impact of maximum air temperature on Blue Crane hatching success in populations occupying hotter climates than the Overberg, e.g., the Karoo and eastern grassland populations. Additionally, it is important that future studies attempt to measure operative egg temperature. This would help us understand how air temperatures translate to operative egg temperatures in the nest, both in the presence and absence of incubating adults. This would aid in better understanding the mechanisms through which high temperatures effect hatching success.

The negative influence of high temperatures on hatching success that I documented in this study is not yet reflected in significant differences between overall hatching success (as measured in 2003/4 (Bidwell, 2004) vs that measured in 2021/2022). A study by Dippenaar (2022) analysed climate data collected between 1990 and 2021 by a weather station within my study area (Boontjieskraal). The study found no significant ($p > 0.05$) increase in annual and monthly mean maximum temperatures over time. This means that, even if high temperatures negatively impact Blue Crane hatching success, this will not reflect in a significant change in hatching success over time, as mean maximum temperatures have not yet significantly changed over time (Dippenaar, 2022). This trend of stable maximum temperatures in the Overberg is however unlikely to persist into the future considering predictions that the relatively cool climate of the Overberg will experience strong regional climate warming (CSAG, 2014). This emphasizes the importance of continued monitoring of the relationship between high temperatures and Blue Crane hatching success, to ensure that interventions are put in place before significance fitness costs are borne by the Overberg population, and the species as a whole.

Relationships between incubation behaviour and hatching success

Another key finding of my study is that the proportion of time adult Blue Cranes spend off their nest during incubation is negatively correlated with hatching success in the Overberg. This is widely supported by studies on other bird species (Larsen et al., 2003; DuRant et al., 2013; Bourne et al., 2020). We know that the degree of adult nest attendance throughout the incubation period influences many aspects of offspring fitness, including hatching success (Larsen et al., 2003; Cooper & Voss, 2013; DuRant et al., 2013). This is because incubation ensures stable temperatures that support embryonic development, while simultaneously buffering the eggs from environmental temperature variation and extremes, as well as microbial infection of the embryos through the eggshell and egg predation (Cook et al., 2005; Shawkey et al., 2009). Conversely, incubation comes at a cost to the adults (Williams, 1993; Williams, 1996; Ardia et al., 2009; Cooper & Voss, 2013; DuRant et al., 2013), which must strike a balance between incubation- and self-maintenance during this phase of reproduction (Cooper & Voss, 2013). This results in varying "incubation rhythms" characterised by the duration and frequency of adult incubation on- and off-bouts. Generally speaking, the greater the nest attendance of incubating adults, the greater the hatching success of a nest (DuRant et al., 2013; Bueno-Enciso et al., 2017; Clauser & McRae, 2017; Bourne et al., 2020). However, there are various factors influencing incubation rhythms, such as adult body condition and breeding experience, weather, predation, disturbance events and nest initiation date (Aldrich & Raveling, 1983; Loos & Rohwer, 2004; DuRant et al., 2013). Additionally, the extent to which off-bouts impact embryonic development and, ultimately hatching success is also highly variable within and among species and environments (Webb, 1987; DuRant et al., 2013; Cooper & Voss, 2013).

Blue Cranes practise biparental incubation, with slightly longer incubation bouts observed in females than males (Allan, 2005). Biparental incubation allows adults to share the aforementioned cost of incubation. This division of labour ensures that, when their partner takes over, adults can compensate for costs incurred during their shift, by increasing foraging while the eggs are protected by their mate (Bulla et al., 2015). The result is that, in species practising biparental incubation, at least one parent is with the eggs almost all the time (White & Kinney, 1974; Vleck, 1981; Biebach, 1986; Silver, 1983; Bulla et al., 2015). However, while Blue Crane nest attendance was high in my study, it was not constant. Of the 33 nests considered, there was only a single nest (3%) for which the portion of time eggs were unattended by adults exceeded 20% (Figure 3a). Thirteen nests (39%) were left unattended for between 10% and 20% and most nests (58%) were left unattended for less than 10% of the time window considered (Figure 3a). I only assessed nest attendance by adult cranes during daylight hours (8:00–16:00), to ensure that camera-trap and focal data correlated. This means that these results do not consider a time window of particularly cold temperatures, where incubation is essential to ensure viable embryos by keeping eggs warm (Ardia et al., 2010; Nord et al., 2010; Nord & Cooper, 2020). And again, because my data do not indicate that maximum air temperature and the proportion of time adults spend off the nest are correlated, it suggests that factors other than temperature extremes are determining the incubation behaviour of Blue Cranes during this period, or perhaps masking the effects of temperature. For example, in other species, the stage of incubation is found to influence adult attentiveness, with fewer extended recesses as the nest approaches hatching date, compared to what is observed in earlier stages of incubation (Loos & Rohwer, 2004). Additionally, studies on other species show that experienced breeding pairs are more attentive overall than less experienced pairs (Aldrich & Raveling, 1983). While these potentially masking factors are intriguing to consider, Julian day, which indicates the stage of incubation, was not supported in my top model, and therefore not included in this analysis. Additionally, the breeding histories of these Blue Crane pairs are unknown.

The most likely cause of unattended nests during incubation is disturbance due to humans or livestock within the agricultural landscape. The influence of human disturbance on incubation behaviour and reduced reproductive success is well-documented, particularly in shorebirds (Safina & Burger, 1983; Baudains & Lloyd, 2007; McGowan & Weston et al., 2011). I struggled to find studies on the influence of agriculture-related disturbance events on incubation behaviour. However, one study on the Upland Goose (*Chloephaga picta*) found that off-bouts associated with human and predator disturbances were significantly longer than those of foraging or livestock-induced off-bouts (Cossa et al., 2018), suggesting that human and predator disturbance is of a greater consequence than livestock disturbance in an agricultural area. While I observed multiple instances of incubating Blue Cranes being flushed from their nest due to the presence of farm workers during my focal observations, it was not possible to determine if or when off-bouts were due to agriculture-related disturbances from the camera trap images. This means that I cannot make any concrete conclusions regarding the impact of human disturbance on Blue Crane incubation behaviour. It is however worth noting that because my nests were spotted from the road, my data may be skewed towards nests that are more exposed to disturbances that nests in more isolated locations.

Bidwell (2004) suggested that reduced hatching success of Blue Cranes nesting in cereal-crop fields compared to pasture was due to increased human activity during harvest time. Again, however, confirming this requires more comprehensive focal data, with adequate sample sizes in each land-use class, which I unfortunately do not have. From a conservation perspective, however, we do know that Blue Cranes in the Overberg have established and flourished in this region despite agricultural disturbances (Pettifor et al., 2009; Hofmeyr, 2012). It also appears that the hatching success of Blue Cranes in the Overberg has not changed since 2004. This means that, even if human disturbance results in longer or more frequent off-bouts of adult cranes, this is not impacting on hatching success at the population level, despite impacts on hatching success at the level of individual nests. That said, we do know that incubation disruption can have other fitness consequences beyond its impact on hatching success (DuRant et al., 2013), and farmer land-use decisions are susceptible to change in response to demand or climate shifts (Altwegg & Anderson, 2009; Pettifor et al., 2009; Davis, 2018) which might result in changes in human activity near Blue Crane nests. It would therefore be interesting to compare the incubation disturbance of Blue Cranes by humans, livestock and predators in the different land-use types, and perhaps consider other measures of fitness impacted by these disturbances e.g., subsequent fledgling survival, in addition to hatching success.

Additional explorations

Failure reason and egg size

In this study, abandoned eggs were significantly larger than the eggs of nests that successfully hatched, however, there was no significant difference in egg size between abandoned eggs those comprising the remaining categories of failed nests (Figure 4a). The difference in egg size between abandoned and successful nests is a surprising result, because the literature indicates that larger eggs are generally associated with a higher hatching success rate and offspring quality (Krist et al., 2011). However, of the four abandoned nests in my sample, two had a clutch size of only one egg. There were only four instances of one-egg clutches in my dataset. Studies on other crane species similarly found far fewer one- egg than two-egg clutches (Nesbitt, 1988; Bradter et al., 2005; Sandar & Choudhury, 2005). This might suggest that rare one-egg clutches are laid by poorer-quality females, with fewer resources to invest in egg production. Eggs in single-egg clutches may still be larger than those in two-egg clutches because those limited resources are not shared with a second egg. The fact that all four one-egg clutches in this dataset failed (two were abandoned, and two predated) may support the idea these clutches might were laid by poorer quality parents. Lower quality adults have fewer available resources to invest in incubation (Krist et al., 2022) which makes them more inclined to abandon incubation. Alternatively, unsuccessful one-egg clutches may not indicate poor quality parents, but rather, a reduced parental investment in single-egg clutches, as the likelihood of a successful breeding attempt is reduced and therefore so too is the incentive to defend the nest or resist external disturbances such as predation events. Finally, there is the possibility that the difference in egg size between abandoned and successful nests is coincidental, and simply an artefact of the small sample size of abandoned nests (n = 4). This is supported by the lack of significant differences in egg size between the other categories of nest outcome (4a).

Failure reason and mean maximum air temperature

This analysis found significant differences in mean maximum air temperatures between the following categories of nest outcome; abandoned nests (n = 4) experienced significantly higher mean maximum air temperatures compared to nests that failed due to other reasons (n = 2), in turn, nests that failed due to other reasons (n = 2) experienced significantly higher mean maximum air temperatures than nests that failed due to predation (n = 6), which themselves experienced significantly higher temperatures than nests that succeeded (n = 25) (Figure 4b). Again, these significant relationships should be interpreted with caution, given the low sample sizes of the nest outcome categories comprising failed nests. Qualitatively, abandoned nests experienced the greatest mean maximum temperature of the nest outcomes considered (Figure 4b). This potentially suggests that adult Blue Cranes abandoned their nests due to unbearable heat loads. This could have been a once-off abandonment event, where adults became too hot and left the nest for good, or perhaps they temporarily left the nest in favour of thermoregulatory behaviours, which left their eggs exposed to fatal heat loads, after which the failed eggs were subsequently abandoned by the parents (McGowan & Weston et al., 2011; DuRant et al., 2019). Perhaps, eggs were left exposed at high temperatures because adults prioritised their own thermoregulatory requirements, or simply did not account for increased heat loads on developing embryos by limiting the duration and frequency of incubation off-bouts at high temperatures (Walsberg & Voss-Roberts, 1983; Webb, 1987; DuRant et al., 2013) Indeed, this may be one of the mechanisms through which maximum temperatures negatively influence hatching success. Although again, if this mechanism is indeed at play, it is not confirmed by my results (Figure 4b). If significantly higher temperatures resulted in nest abandonment, I would expect to see significant differences in mean maximum temperature between abandoned nests and all of the other nest outcome categories. Instead, my data only shows significant temperature differences between pairs of nest outcome categories, indicating that if a biologically relevant relationship between temperature and nest outcome is present, my data lacks sufficient power to pick up on it.

Failure reason and incubation behaviour

Failure reasons comprised "abandoned" nests, where adults abandoned intact clutches, "predated" nests, where eggs were destroyed by predators and "other" which included nests that were crushed by a farm vehicle (n = 1), or at which the cause of nest failure was unknown (n = 1). Parents of nests that failed due to predation, left their eggs unattended for significantly longer periods of time than parents of nests who eventually abandoned their clutch. Adult cranes actively defend their nests from predators, which means that, in their absence, eggs are undefended and more vulnerable to predation. This is an additional potential mechanism through which less attentive incubation results in reduced hatching success. However, were this mechanism at play, I would also expect to see that predated nests were left unattended for significantly longer periods than successful nests, which these results do not indicate. This suggests that my data lacks the sufficient power to confirm the existence of potentially relevant biological mechanisms behind significant differences in parental incubation behaviour and nest outcome. All three of my additional analyses on nest outcome indicate a potential influence of egg size, mean maximum temperature and adult incubation behaviour on nest outcome, though my data lack the power to confirm these effects and, should they exist, the biological mechanisms possibly behind these effects. Future studies should consider the same categories of nest outcome, and combine those data with these, so as to increase statistical power to find biologically relevant trends.

4. Conclusion

Hatching success in the Overberg Blue Crane population appears unchanged since 2004. Therefore, the change in the Overberg Blue Crane population trajectory since around 2010 is likely due to other factors such as adult breeding effort, or juvenile or adult survival. It was difficult to find an adequate number of nests for this study. Even over the course of two field seasons, I found only 56% of the number of nests that Bidwell (2004) found in a single season in the same region. This itself suggests reduced Blue Crane breeding pair densities since 2004. Subsequent studies on breeding Blue Cranes in the Overberg should account for these reduced densities by increasing the search effort, perhaps by including more nest searchers and searching a larger area or more comprehensively across private farmland which may be possible with increased farmer engagement and awareness of the issue. Land-use class did not influence hatching success, though this non-significant finding could be due to the low sample size of cereal- crop nesters. Mean maximum temperatures had a significantly negative impact on hatching success despite the relatively low maximum temperature recorded during the study. This suggests that predicted regional climate warming may impact the overall hatching success, and in turn, fitness, of the Overberg Blue Cranes and most likely other key populations. This finding is therefore of particular conservation concern for the species, and future studies are essential. Incubation behaviour, summarised by the proportion of time eggs were left unattended during incubation, has a negative impact on hatching success, possibly due to the increased predation risk of undefended eggs. These findings will help direct future studies aiming to understand the population trajectory of the Overberg Blue Cranes, and how the population dynamics might be impacted by climate change and land-use change.

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