

The Effects of Climate Change on the Breeding Ecology of African White-backed Vultures

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Table of contents

1	Declarations	2
2	Acknowledgements	3
3	Abstract	3
4	Introduction	4
4.1	Aims and Objectives	10
5	Methods	11
5.1	Study Area	11
5.2	Data collection	11
5.2.1	Field data collection	11
5.3	Data Analyses	13
5.3.1	Weather data	14
5.3.2	Statistical analyses	16
6	Results	23
6.1	Objective 1: Number of Active Nests	23
6.2	Objective 2: Breeding success	28
6.3	Objective 3: Breeding timing of successful nests	32
7	Discussion	36
A	Appendix	42
	Bibliography	45

1 Declarations

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2 Acknowledgements

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3 Abstract

Evidence suggests that weather conditions have an influential role in shaping the population dynamics of many avian species by affecting key demographic rates and important life-history events. Weather can affect avian reproduction through multiple pathways, such as direct exposure to stress-inducing conditions or indirectly, through changes in food availability and energy balances. As climate change is projected to increase weather variability, it is important to understand how annual variation in weather is shaping reproductive cycles, especially in long-lived species where repeated disruptions in reproduction have population-level consequences. This study investigated how, weather influences the different breeding stages of African White-backed vultures (*Gyps Africanus*), by using 31 years of breeding data from Dronfield, Kimberley. The relationships between weather and the number of active nests, breeding success, and breeding timing formed the main focus of this study. Candidate models were fitted for each breeding stage and compared using an information-theoretic framework (AICc). The number of active nests indicated high annual variability, which was mainly explained by the long-term temporal trends, with weather adding minimal explanatory power. Breeding success showed a positive association with minimum temperature, which explained 21 % of the between-year variability after accounting for the temporal structure. Lagged effects of annual rainfall in the previous year had the strongest association with the between-year variation in breeding timing. The results suggest that the effects of weather on reproduction is not uniform across the breeding stages but affect each stage in a distinct manner and are likely to operate alongside other temporal processes.

4 Introduction

Weather is an important driver of population dynamics across many taxa by influencing key demographic rates and the timing of important life-history events (Chase et al. 2005; Knape and Valpine 2011; Morris et al. 2020). Sæther et al. (2004) summarised evidence across many bird populations to show that weather influences population dynamics by having effects on key demographic rates such as survival and reproduction. Additionally, they emphasised that weather typically has varying influence on different life-history stages and processes, such as migration, breeding or moulting (Sæther et al. 2004). Each of these demographic rates and life-history stages responds differently to weather conditions, and responses are typically shaped by changes in the energetic balances and food availability, which influences individual condition, survival and breeding investment (Sæther et al. 2004; Grosbois et al. 2008).

Climate variability typically results in more frequent fluctuations in abiotic conditions. In turn, these fluctuations increase the unpredictability of the environment and result in the variability of biological responses, including survival rate, fitness and phenology of many organisms and ecosystems (Weiskopf et al. 2020). Despite often being an overlooked driver of environmental change, persistent annual variation in climatic conditions could result in direct consequences for species persistence and broader population dynamics (Vázquez et al. 2017; Berzins et al. 2020). The way in which organisms and ecosystems respond to climatic variation is an important mechanism that could aid in predicting how climate change and increased variability could influence biodiversity (Maclean and Wilson 2021; Cockrem 2022), as climate change is projected to intensify in the future (Thornton et al. 2014).

Most organisms are adapted to specific temperature and precipitation ranges, and as weather conditions move away from the optimum, it often leads to consequences for the species distribution, growth, reproductive success and survival (Elkins 2010). Climate change and variability alter key environmental cues by shifting rainfall and temperature regimes, which could cause significant disruptions to the geographical distribution, reproduction, muration, migration, survival and other important processes of many species (Inouye 2022). In the event of increasing temperatures, for example, processes such as the reproductive timing and migration have advanced (Taff and Shipley 2023). Although these phenological shifts could help animals adapt to the changing environment, this often causes other ecological processes or food availability to fall out of sync with breeding, which could reduce the fitness and reproduction of individuals (Visser et al. 2004; Carey 2009; McDermott and DeGroote 2016; Inouye 2022).

Alongside many other animal species, avian populations are susceptible to the consequences of unpredictable variation in climatic conditions as they heavily rely on specific environmental conditions to regulate important life-history processes such as reproduction, migration and foraging efficiency (Shepard and Lambertucci 2013; Mainwaring et al. 2021). Thus, global climate could both directly and indirectly have an effect on avian populations through any life-history process (Cockrem 2022). The direct effects of weather on avian populations typically involve immediate physical consequences of weather conditions, such as rainfall and changes in thermal conditions, which could directly influence the survival of individuals (Schreiber 2002). Additionally, weather conditions affect the metabolic rate of many bird species by typically increasing the energetic cost while trying to adapt to fluctuating conditions and extreme conditions such as intense storms, prolonged heatwaves, droughts and excessive chilling events (Crick 2004). In contrast, indirect effects of weather are typically driven by broader scale changes such as food abundance or habitat loss that influence survival and other demographic rates, such as reproduction (Schreiber 2002). Jenouvrier et al. (2013) presented evidence of mostly indirect effects on population dynamics of multiple seabird species, where they emphasised the effects of varying weather conditions on the breeding success and survival of individuals through the loss of breeding habitat and food availability, rather than direct effects (Jenouvrier 2013). Similarly, lower breeding success in mourning doves (*Zenaida macroura*) was linked to changes in rainfall, which created inhospitable nest conditions and reduced foraging efficacy of adult birds (Osborn 2023).

Reproduction is one of the most energetically demanding life-history stages across many bird species, making it particularly sensitive to climatic variability (Griebel and Dawson 2019; Andreasson et al. 2020). The reproductive success of many avian species therefore relies on resource availability, often shaped by climatic conditions (Arct et al. 2025). If the climatic conditions limit resource availability, reproduction increases in energetic cost with limited gain, which poses significant challenges to the successful egg laying, incubation and parental care (Andreasson et al. 2020). In this case, the effects of weather are influencing reproductive success indirectly by introducing limitations to the energy balance and ability to access food. In addition to the high energetic cost, conditions that result in reduced resource availability can cause birds to change their breeding strategies by choosing not to breed during the season entirely, changing their breeding timing, or reducing the parental investment if the cost becomes too high (Sauve et al. 2021). The effects of temperature on the reproductive output of avian species has largely been the focus point of how weather affects reproduction, however, the effects of varying rainfall patterns are also important (Sparks et al. 2002; Fogarty et al. 2020). Similarly to the high energetic cost of thermal stress, unpredictable rainfall regimes can directly affect foraging efficiency, food availability and cause prolonged periods of energetic expenditure (Larson et al. 2015), leading to reduced investment in parental care and therefore reduced breeding success.

Together with the indirect effects, weather can also influence reproductive output by directly adding physical challenges across the early life stages including egg development to fledgling. These constraints include possible hypothermic and hyperthermic events for chicks as during this early life-stage, their thermoregulatory ability is underdeveloped (Kosicki 2012). Additionally, in more severe instances, prolonged periods of rainfall could cause nest flooding, which often causes nest collapse or the drowning of chicks (Ortega et al. 2022). Conditions deviating from the optimum for chick survival, could significantly reduce the breeding success of avian populations. A study conducted by Dawson et al. (2000), on the relationship between reproductive success and weather conditions for Kestrels found that in the event of inclement weather, there were significant impacts of the reproductive success. During these unfavourable conditions, the nestlings were notably smaller in body mass which decreased the probability of surviving to a fledgling compared to nestlings during more stable conditions (Dawson and Bortolotti 2000).

The decision of when to initiate breeding is a key component to the life-history of many avian species, and strong evidence suggests climate change has significant impacts on the timing of breeding (Fletcher et al. 2013; Harriman et al. 2017; Dunn and Winkler 2019; Zwaan et al. 2022). Weather conditions during the pre-breeding period, both shorter and longer-term conditions, often influence breeding initiation (Grudinskaya et al. 2022). It is known that temperature influences breeding timing with warmer temperatures often shifting egg-laying earlier in the breeding season through behavioural responses to warming conditions (Niffenegger et al. 2025). In addition, breeding timing is often influenced by a carry-over effect of conditions experienced throughout the year, and not just during the early breeding season (Zwaan et al. 2022). At the start of each breeding season, the body condition of the breeding birds may vary depending on the conditions they have experienced throughout the year, which could affect breeding timing or the likelihood to breeding (Blums et al. 2005). However, the ability to delay or skip breeding is predominantly seen in longer-lived birds, as birds with lower adult survival are unlikely to skip a breeding season even when the conditions are poor because of limited future reproduction opportunities (Verhulst and Nilsson 2008). Instead of not reproducing at all, short-lived species often respond to their environmental conditions by adjusting when they breed, however, this strategy could lead to reduced fitness (Visser et al. 1998). Delaying breeding can reduce the survival of adult birds, as seen in the experimental case of collared flycatchers (*Ficedula albicollis*), where costs arise because breeding later in the season in response to unfavorable conditions leaves less time for processes such as moulting, which affects survival (Visser et al. 1998). Currently, relatively little is known about the drivers of breeding timing in birds that live in environments that are not driven by temperate seasonality. Monajem and Bamford (2009) presented an example of what drives breeding timing in a southern African system. Their results indicated that rainfall effected both breeding timing and success of Marabou Storks (*Leptoptilos crumeniferus*), where

breeding success was decreased with increasing rainfall (Monadjem and Bamford 2009). This suggests that rainfall may be a key driver in the breeding outcome of species in semi-arid systems.

If adult birds are experiencing decreased body condition, they are more inclined to delay breeding or will not initiate breeding entirely for the breeding season (Zwaan et al. 2022). Alongside reduced body condition, more frequent or prolonged storm events often lead to delaying the laying date, or no breeding at all (Dunn and Winkler 2019). Intense wind speeds could lead to delayed breeding timing by reducing the foraging efficiency of many bird species, particularly those that use thermals for their flight, like vultures. In contrast, rainfall events often signal breeding initiation and birds often initiate breeding during, or just before, rainfall events, as it provides more certainty of increased food availability post rainfall (Dunn and Winkler 2019). This is especially the case in arid systems, where there is often high variability in climatic conditions and is typically characterised by sporadic rainfall events (Noy-Meir 1974). For birds inhabiting arid environments, like the sociable weaver (*Philetairus socius*), rain functions as the primary signal for breeding, and breeding typically does not occur in the absence of rainfall (Maclean 1973).

When a population experiences low breeding investment, decreased breeding success or the loss of entire breeding seasons, the population could face a drastic decline, which is particularly threatening to long-lived species such as vultures. For these species, the long-term viability of the population relies on the repetition of successful breeding seasons due to their delayed maturity and reproductive rates (Andreasson et al. 2020).

Across the globe, there are 23 vulture species, and while some species are range restricted, a large number of these species are found across multiple continents (Ogada et al. 2012). Vultures are considered to play a vital role in maintaining the health of entire ecosystems through their role as specialised terrestrial scavengers and recycling large amounts of organic waste within an ecosystem (Carucci et al. 2022). Vultures can swiftly locate and consume carrion, and by doing so, they create competition for and control other often problematic scavenger populations such as jackals and rodents (Buechley and Sekercioglu 2016). Through their quick disposal of carrion, which acts as a reservoir for harmful diseases such as rabies and anthrax, vultures limit the spread of these pathogens into the ecosystem (Ogada et al. 2012). Thus, the absence of vultures, or a large decline in vulture populations, could have significant consequences on the health and, therefore, overall productivity of ecosystems.

Despite their ecological importance, vultures are considered one of the most threatened avian groups across the globe, with rapid declines in populations documented for most of the species (Overveld et al. 2020). Threats to vulture populations include pesticide and lead poisoning, powerline collision, habitat loss, and

disturbances during breeding, such as limited food availability and increased sporadic weather events (Ives et al. 2022). Vultures are large-bodied birds, known for high flight speed, increased foraging ranges and the important ability to store energy reserves in the event of scarce food availability (Ogada et al. 2012). In addition, vultures are also known for their slow life history strategy, focusing on long-term survival, growth, parental investment and include delayed maturity and low reproductive rates (Perrig et al. 2019). Adult vultures have a relatively high survival rate, typically above 80%, compared to juveniles and chicks, with no clear indication whether that differs between male and female birds (Mundy et al. 1992). These life-history traits make vultures especially vulnerable to reduced reproductive success, which has long-term consequences for future population stability.

The African white-backed vulture (*Gyps africanus*) is the most widespread and common vulture species across Africa, and as tree dwellers, these vultures are typically found in wooded savannah and bushfield areas (Mundy et al. 1992). White-backed vultures are classified as critically endangered by the IUCN Redlist because of the rapidly declining population (IUCN 2021). Currently, there are approximately 4000 breeding pairs of white-backed vultures, and they typically nest at the top of small to medium-sized scattered woody trees such as camelthorn (*Vachellia erioloba*) in southern Africa (Mundy et al. 1992). White-backed vultures are monogamous, and during a breeding season, one egg is laid between April and July in Southern Africa and laying occasionally extends to September in areas of West Africa (Houston 1976; Mundy 1982). Thereafter, the egg is expected to hatch after roughly 60 days, and chicks take around 130 days to reach fledgling. This is then followed by parental care from both parents for about 6 months after the chick has fledged. Depending on the region, the breeding success of white-backed vultures is highly variable, ranging from 40-90% (Mundy 1982).

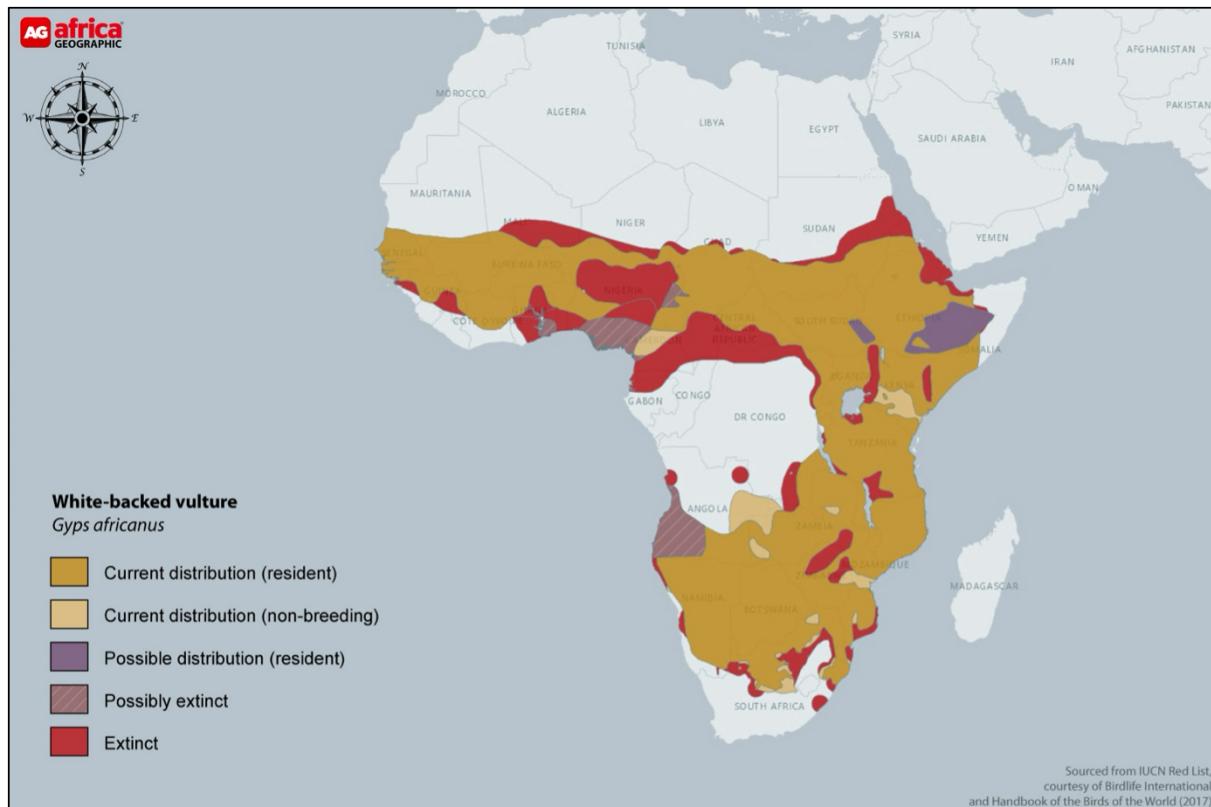


Figure 1: A map showing the distribution of African White-backed vultures (*Gyps africanus*) across Africa based on the IUCN Redlist range data (BirdLife International and Handbook of the Birds of the World 2017).

Conway et al. (2015) predicted that Southern Africa will experience significant shifts in climatic conditions, including increased temperatures and changing rainfall patterns, causing major shifts in climatically suitable habitats for numerous species. Additionally, projections show a general drying of many parts of Southern Africa, including summer rainfall areas, most relevant to White-backed vultures (Conway et al. 2015; Engelbrecht et al. 2024). Similar to other large-bodied birds, vultures rely on atmospheric thermals for efficient soaring to locate food, which could become constrained when there is an increase in rainfall that suppresses the formation of these thermals (Virani et al. 2012). Constraints like these could cause vultures to reduce their breeding activity and therefore alter their population dynamics because food availability is one of the most important factors that cause variation in the reproductive success of avian species, as they often time their breeding to correspond with high food availability (Harriman et al. 2017). These effects are typically seen in years that are known for prolonged rainfall events, and the lasting effects of reduced foraging efficiency are reflected throughout the breeding season.

4.1 Aims and Objectives

This study aims to assess how inter annual weather variation influenced the breeding ecology of African white-backed vultures by using 31 years of breeding data from Dronfield Nature Reserve in Kimberley, South Africa. Three components of the breeding cycle will be assessed for a comprehensive overview what influence weather has, namely, the number of active nests, proportion of successful nests and the breeding timing of successful nests. The study will address three objectives:

1. To assess whether annual weather variation is associated with varying number of active nests of white-backed vultures

We hypothesise that the number of active nests of white-backed vultures will be reduced in years with weather conditions characterised by higher annual temperatures wind, prolonged rainfall and increased storm events.

2. To assess whether annual weather variation is associated with varying breeding success of white-backed vultures, measured in the proportion of active nests that produce a fledgling.

We hypothesise that the breeding success of white-backed vultures will decrease in years of weather conditions characterised by higher annual temperatures wind, prolonged rainfall and increased storm events, due to lower reproductive investment.

3. To assess whether annual weather conditions in the pre-laying period, and conditions of the previous year are associated with variation in breeding timing of white-backed vultures.

We hypothesise that the breeding timing, measured in laying dates, is influenced by the weather conditions in the 30 days prior to laying periods, which reflects white-backed vulture sensitivity to environmental cues before breeding.

Currently, very little is known about how climatic variability is affecting breeding patterns of white-backed vultures, a critical gap this study aims to fill. This study therefore aims to provide clarity on how inter annual weather variability influences key components of the breeding ecology of white-backed vultures and to contribute to the growing body of research that investigates how weather variability is shaping avian reproduction, rather than focusing on the effects of shifts in mean conditions alone.

5 Methods

5.1 Study Area

The breeding data used in this study were collected at Dronfield Nature Reserve, approximately 5km north of Kimberley in the Northern Cape, South Africa. Dronfield is part of a greater portion of protected and farming landscape, allowing vultures to regularly move between breeding and foraging areas. Dronfield is located within a semi-arid region with a dominant vegetation type, the Kimberley Thornveld and has a mean annual rainfall of approximately 400 mm. The Thornveld is known for its open savanna structure with camel thorn trees scattered across the landscape with tall grasses in between. In addition, Dronfield includes numerous areas of semi-open mixed woodland, which, in combination with the savanna structure, supports a long-term breeding population of white-backed Vultures (*Gyps africanus*). The nests of more than 100 White-backed vulture breeding pairs are mainly found within medium to large camel thorn trees (*Vachellia erioloba*) found across the reserve. This breeding colony is one of six in the greater Kimberley area, with relatively few threats while under Dronfield management. However, the threat of powerline electrocution is persistent as multiple powerlines run across the reserve. Additionally, when these vultures leave the reserve, they are faced with numerous surrounding threats, such as food shortage due to land use change, poisoning, including lead poisoning associated with hunting activities and drowning in steep-sides reservoirs, while foraging in surrounding farmlands. The consistent distribution of suitable nesting habitats at Dronfield resulted in a consistent spatial distribution of nest sites across the years, allowing for repeated long-term monitoring of the individual nest sites.

5.2 Data collection

5.2.1 Field data collection

The long-term monitoring program of African white-backed vultures commenced in 1993, with few methodological adjustments made to date. The primary goal of the monitoring program has been to document the population dynamics and breeding activity of the African white-backed vulture population in the reserve, with a specific focus on breeding success and effort across the years. These surveys were conducted by experienced observers, each ensuring standardised protocols for nest identification, assessment, and recording of breeding data using the same data sheets.

The surveys were predominantly conducted twice a year, during the breeding season, including an early breeding survey and a post-breeding survey. Egg laying at Dronfield typically occurs from the April/May to the beginning of June. Therefore, since 2001, the early breeding survey has been conducted just after this stage of the breeding cycle, in August, prior to this, sampling was conducted in October. Vegetation cover during this time also allowed for easier visualisation and access to the nests in the tree canopy. This survey aimed to establish annual number of active nests during the breeding season. To do this, multiple teams were deployed and assigned a section of the reserve to ensure comprehensive spatial coverage. Survey routes were established to ensure coverage of all previously known nesting areas, including additional suitable habitat to record any new nests that might have been established. En route, the various teams visited and assessed each tree for vulture breeding activity, including the presence of parents at the nests as incubation commenced, the presence of an egg inside the nest, or no indication of breeding activity at all. The search area remained constant over the duration of the study period.

Active nests were then defined as nests that had clear evidence of breeding activity for the current breeding season, such as a recorded egg inside the nest. Preparatory breeding activity, such as nests with evidence of recent preparation and lining, but without an egg, were documented as a breeding attempt to account for later egg-laying that could have occurred after the survey. The nests that showed no sign of any breeding activity were classified as inactive nests. The observation date, tree number and coordinates were documented alongside active or inactive identification of nests within the reserve to enable long-term nest use of each new or recurring nest.

The post-breeding survey was conducted in October and aimed to assess the breeding outcome, following the number of active nests survey in August. This survey allowed us to determine the breeding success of the nests identified as active in the October survey by establishing the presence of a surviving chick in the nest. In October, the chicks were large enough to be fairly certain that they will fledge, however, no chicks were old enough to have fledged yet. Each nest identified during the first survey in August was revisited and assessed for its breeding outcome. For a nest to be classified as successful, a living chick had to be present in the nest during the time of surveying. The chicks in these nests were then carefully retrieved from their nests to conduct additional measurements before being placed back into their nests. This included measuring individual weights and the wing length of each chick to establish an estimated laying date, used to analyse changes in the annual breeding timing. To estimate the chick age, wing length was used as a proxy for chick age as it provides a measure of age during early development based on established wing growth curve from southern African vultures (Mundy 1982). Based on the wing length, the estimated age of each chick was then subtracted from the

observation date to establish relative laying dates. Additionally, each chick that was deemed the appropriate size was ringed and tagged, receiving a unique code for long-term monitoring. Nests that were identified as active during the August survey but did not contain a living chick during the October survey were classified as unsuccessful nests, typically adjacent to evidence of eggshell fragments or whitewash. No timing data could be recorded for unsuccessful nests based on the method used for successful nests, and therefore, our analyses of timing only included the successful nests.

During both of these surveys, a standardised nest status code was assigned to each nest (Appendix Table A1). A list of 20 different codes was constructed to describe what is seen at each nest sighting, ranging from breeding outcome, nest condition and other notable sightings at each nest that could describe the breeding activity at each nest. This code system was kept consistent throughout the monitoring program. The main aim of the monitoring program remained the same over time, however, the survey design has been adjusted to ensure the most effective way to capture breeding activity in the reserve. The initial surveying years, 1993 to 2000, consisted of a single survey in October to document the number of successful nests during that breeding season by the presence of chicks. From 2001 onwards, the second survey, in the early-breeding period, was introduced to improve and ensure more robust data collection regarding breeding activity at Dronfield. Therefore, breeding success was only inferred from 2001, onwards.

5.3 Data Analyses

I analysed the relationship between annual weather variation and the breeding performance of African white-backed vultures using the long-term data collected at Dronfield. Moreover, I examined how the weather affects three main aspects of the reproductive cycle, including the number of active nests, breeding success (proportion of nests that produced a fledgling) and breeding timing (assessed using estimated laying dates). To determine if there were any long-term temporal trends in the breeding cycle stages, exploratory analyses were conducted. The number of active nests and breeding timing were assessed using linear models and breeding success was analysed using generalised linear model. All statistical analyses were conducted in R statistical computing environment (R version 4.4.1) (R Core Team 2024).

5.3.1 Weather data

The weather variables used in this study were derived from a package in the program R 4.4.1, rnoaa, by specifying the weather station ID most suitable for our data (R Core Team 2024; Chamberlain and Hocking 2025; Sparks et al. 2025). The weather variables were collected from the Kimberley meteorological station, 10 km from our study area, Dronfield. The variables used in the analyses were selected to represent a broad understanding of the climatic variation experienced at Dronfield and were biologically motivated. To broadly classify the variables seen in Table 1, rainfall, temperature, wind and hail were assessed for their impacts on the three outlined focus areas of the breeding cycle.

Using the daily weather records derived from the Kimberley meteorological station, annual summaries (January to December) were calculated for each year, from 1992 to 2025. Temperature variables were summarised as annual mean and maximum temperatures. Similarly, rainfall variables were summarised as the total annual rainfall, maximum daily rainfall and the number of rain days in each year. Wind speed was summarised as maximum, and mean wind speed each year. Hail was summarised as the number of hail days present in each year. When analysing the breeding timing, the weather variables were summarised over March each year, creating a fixed window for the weather summaries used to analyse breeding timing. In this study, lagged effects of weather conditions were of interest, and therefore annual lagged weather (one-year lag) variables were derived from the annual summaries to represent the general conditions of the previous year.

Pearson correlation coefficients were used to determine the correlations between the predictor weather variables. The temperature variables showed strong correlations with one another, and similar correlations were observed among the rainfall variables. Wind variables showed moderate correlations with one another and weak correlations to temperature and rain. Hail was weakly correlated with all of the other variables. See appendix for more detail on the correlations between weather variables. Temporal trends in weather variables were assessed using time-series plots (Appendix Figure A1). The main temporal trends seen are in temperature and hail days, showing a weak increase over time with precipitation and wind variables showing no consistent increase or decrease over the years.

Table 1: The weather variables and their biological motivation that were used to assess the effects of weather on the breeding ecology of Africam white-backed vultures at Dronfield Nature Reserve, Kimbereley.

Weather variable	Justification
Minimum temperature	Cold temperatures during incubation and the nestling stage may cause direct mortality and increase energetic costs for adults, potentially influencing the decision to initiate or maintain breeding.
Maximum temperature	High temperatures may cause egg or nestling mortality due to heat stress and dehydration.
Mean temperature	Integrated measure of overall thermal conditions, which may influence adult energetic balance and, consequently, breeding performance.
Number of rain days	High frequency of rainfall events may reduce adult foraging efficiency and limit chick provisioning, independent of total rainfall amount.
Total rainfall	Prolonged wet or dry conditions may influence food availability through effects on vegetation and carcass detectability, indirectly affecting breeding performance.
Maximum daily rainfall	High-intensity rainfall events may cause nest flooding or exposure and reduce adult foraging efficiency during critical breeding stages.
Maximum wind speed	Strong wind events may cause nest damage or collapse, leading to egg or chick mortality.
Mean wind	Prolonged windy conditions may increase energetic costs through increased thermoregulation and reduce adult foraging efficiency.
Hail days	Hail events may cause direct injury or mortality of eggs and nestlings and increase the risk of nest failure.

5.3.2 Statistical analyses

The objectives were analysed separately by using specific statistical models deemed fit for the structure of the response variable. This was done by adopting a candidate model set approach for each objective, where the different models represented a biologically motivated hypothesis of how the selected predictor variables might affect each stage of the breeding cycle (Burnham and Anderson 2002; Grace and Irvine 2020; Nichols and Cooch 2025). The candidate model sets were set before the analysis was conducted based on what was known about vulture ecology and inference of possible causal relationships. Models that were thought of once the analyses has started, were treated separately and were clearly labeled as a-posteriori models. A set of directed acyclic graphs (DAGs) was constructed to support causal inference by providing clarity on the assumed relationships between weather variables, time (year), unobserved ecological processes and the different breeding responses, which ultimately were used to help interpret the model decisions (McElreath 2018). Each DAG represents a plausible causal structure of how different variables could influence the breeding response. In each graph, the squares are called nodes and represent the observed variables in the causal structure with arrows representing the hypothesised causal effects. When nodes are not joined by an arrow, it implies that it is assumed that there is no direct causal connection between the these nodes. The round nodes in some of the causal structures, represent unobserved variables. DAGs were visualised using package DiagrammeR (Iannone and Roy 2024), and other visualisations were done using tool in the package tidyverse (Wickham et al. 2019).

Single predictor models were inferred by the weather variable selection justified above (Table 1). Models including combined effects of certain variables were constructed to represent interactive climatic processes that could shape each stage of the breeding cycle. For the additive models, temperature variables and rainfall were combined to represent the influence of the combined effects of thermal conditions and other plausible weather conditions that in combination, effects foraging efficiency, energetic demand and direct nest exposure. In addition, combining rainfall and wind into a model represented conditions that were likely to cause physical disturbance to both adult birds, and the nests. Interactions between weather variables were also added to the models, however, only when there was a clear idea of how the one weather variable could influence the effect of the other. This could occur when the effects that temperature has on the breeding success, is increased by the prolonged periods of rainfall or strong winds.

A model selection approach was used, which involved fitting the set of priori models and then calculating the sample size-adjusted Akaike's Information Criterion (AICc) for each one using the package, AICcmodavg

(Mazerolle 2023). Models that have smaller AICc values were considered as stronger support models. The candidate models were then ranked by the difference in their AICc values (ΔAICc) relative to the best supported model for each objective to identify which weather predictor, or combinations of predictors, better explained variation in each breeding response.

Because of the continuous nature of both breeding timing and the number of active nests, these two objectives were analysed using linear regression models. The number of active nests was log-transformed before conducting the analyses to adhere to model assumptions, whereas breeding timing was deemed normally distributed before fitting the models. The breeding success objective was analysed using binomial generalised mixed models using a logit link function and package lme4 (Bates et al. 2015), as breeding success is measured as the proportion of successful nests relative to the total number of nests each breeding season. After the best supported weather model has been identified, an a-posteriori analyses was conducted by fitting the best model with the number of active nests, used as a proxy for population size, as a covariate, corresponding with causal scenario represented by Figure 3d.

Figure 3d represents the plausible scenario where an unobserved variable acts as a confounder, which effects both breeding timing and breeding success.

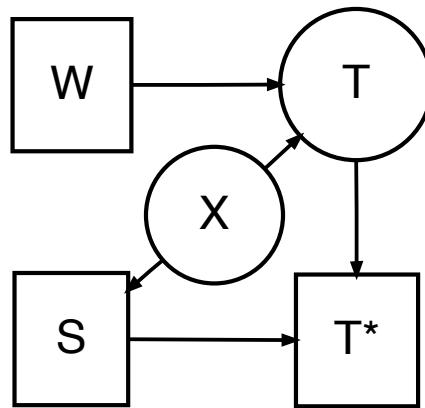


Figure 3d: Directed acyclic graph showing a causal structure between the breeding timing of successful nests, weather (W), success (S) and observed timing (T^*) and population size (X) in Scenario D.

In Figure 3d, an unobserved variable (X) influences both breeding timing (T) and the breeding success (S). Its effects on both processes makes it a confounder which means that the effect of the weather variable of interest on the observed timing cannot be understood without accounting for the shared influence. If X were observed and included in the model, our results could be unbiased estimates of how the weather variable of interest,

effects the breeding timing (Cinelli et al. 2024). By accounting for this unobserved variable, the confounding pathway is blocked and allows clearer causal inference. A plausible candidate for the unobserved variable is population size, which could influence both breeding timing and breeding success through different pathways such as density-dependent constraints (Carrete et al. 2006; Fernández-Bellon et al. 2016). Despite true population size not directly observed, the number of active nests provides a reasonable proxy for population size, therefore, the number of active nests was included as a covariate in selected models.

Year was added as a random effect to the models to account for overdispersion in the data which was assessed using diagnostic tools in the performance package (Lüdecke et al. 2021). By using the proportion of successful nests, it accounted for the variation in sample sizes across the multiple breeding seasons. The between-year variance explained by each predictor variable was calculated as the change in the variance of the temporal random effects. The intercept-only model, without covariates, the variance represents the total temporal variance (σ^2) in the breeding success. When covariates were added to the models, the variance of the random effect represents the remaining temporal variance that is not explained by the covariate (σ_{res}^2). The percentage of the variance explained by the covariate is then calculated as $(\sigma^2 - \sigma_{\text{res}}^2)/\sigma^2$

For the number of active nests, the explanatory analyses showed a clear temporal trend and year was included as a numerical variable to account for the gradual temporal trend throughout the study period. The number of active nests were modelled with, and without year as a covariate to be able to compare the effects of the weather variables under different causal assumptions. Additionally, this method allowed us to detect associations between weather and the number of active nests, after the strong temporal trend was accounted for. To determine how this temporal structure could influence interpretation of weather effects, alternative causal assumptions were made using directed acyclic graphs seen in Figures 2a - 2c. Models were then fitted with and without year to reflect these alternative causal structures and to compare the effects of weather under alternative assumptions regarding the confounding and mediation effects of the temporal trend.

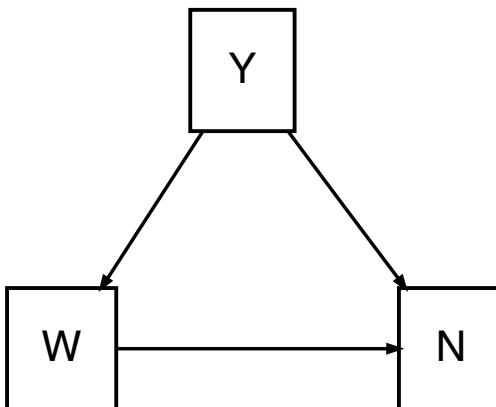


Figure 2a: Directed acyclic graph showing a confounded causal structure between the number of active nests (N), year (Y), and weather (W).

In Figure 2a, the scenario represented how the temporal trend (Y) directly influences both weather (W) and the number of active nests (N). Because Y affected both variables, it acts as the confounder of the weather-breeding relationship. Therefore, to estimate the direct effect of weather on the number of active nests, it was necessary to control for Y in the analysis.

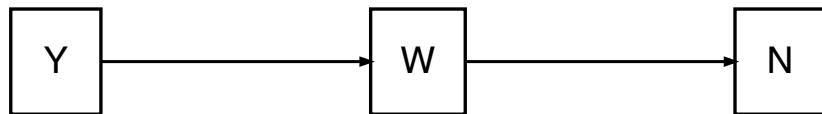


Figure 2b: Directed acyclic graph showing a causal structure the number of active nests (N), year (Y) and weather (W).

In Figure 2b, the scenario represented how the temporal trend (Y) influenced the weather variable of interest (W), which in turn, affected the number of active nests (N). Time trend did not directly have an effect on the number of active nests, meaning Y is not a confounder of the weather-breeding relationship. Controlling for Y was therefore not needed as it acted through weather.

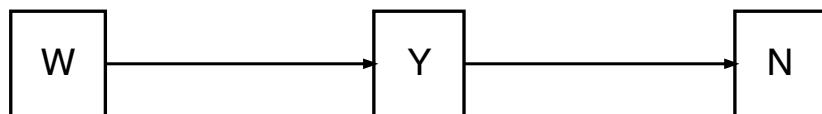


Figure 2c: Directed acyclic graph showing a mediated causal structure between the number of active nests (N), year (Y), and weather (W).

In Figure 2c, the scenario represented how the temporal trend (Y) acted as a mediator of the weather effects on the number of active nests, where weather itself can exhibit a time trend which drives changes in N, year influenced the number of active nests. Because year is in between weather and the number of active nests in the causal pathway, controlling for year would have blocked off the effects of interest completely (Cinelli et al. 2024). Therefore, to estimate the total effects of weather on the number of active nests, year should not be included as a control.

The main focus of the breeding timing was to identify the effects of weather during the pre-laying window and which variables acted as a cue to initiate breeding, therefore year was not included in these models as a predictor variable. To assess the effects of weather in the pre-laying period, weather variables were summarised for a fixed window, the whole month of March. This ensured that all of the nests within the same breeding season, were associated with the same weather conditions which allowed for between-year comparison of laying date, rather than between nests in a given season. The variables were derived from daily meteorological observations and prior to the analyses, the means of temperature and wind speed variables were summarised. Rainfall was summarised as totals with the number of rain days and hail days as counts. The laying date was only available for the successful nests (T^*), as the unsuccessful nests lacked the information needed to estimate laying date (T). The implications of this missingness depends on the assumed causal structure (McElreath 2018), and two alternative structures were considered as seen in Figure 3b and 3c.

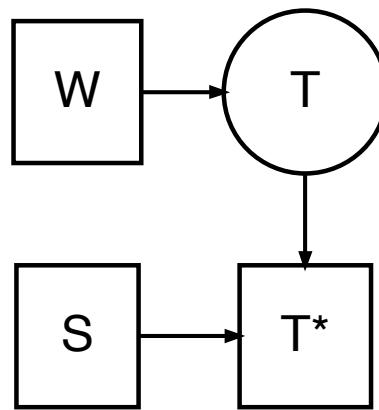


Figure 3a: Directed acyclic graph showing a mediated causal structure between the breeding timing (T), weather (W), breeding success (S) and observed timing of successful nests (T^*) under scenario A. Breeding timing of all nests are unobserved, therefore represented as a circle in the DAG.

In Figure 3a, this DAG a causal scenario where the successful nests are a random subset of all nests, with respect to the weather variable I'm interested in. In this case, bias only occurs if the interested weather variable used to explain timing also has effects of the breeding success. Under this scenario, the weather variable of interest affects the breeding timing, but not the success and as a result, the analyses of timing of successful nests gives a valid inference about the effects of the specific weather variable on breeding timing.

The causal scenario represented by Figure 3b, the weather variable of interest influences both timing and breeding success and the timing is only observed for the successful nests.

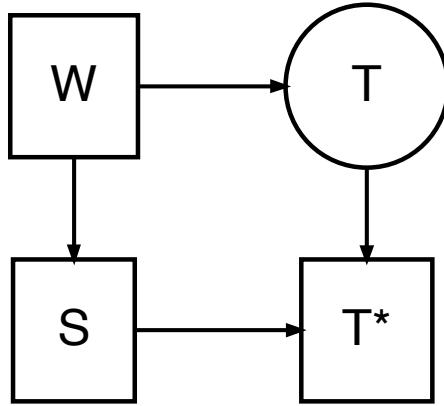


Figure 3b: Directed acyclic graph showing a causal structure between the breeding timing (T), weather (W), success (S) and observed timing (T^*) under Scenario B.

In Figure 3b, the graph represents a scenario where weather (W) influenced both breeding timing (T) and breeding success (S) but timing does not have a direct causal effect on success. therefore, success is associated with weather (W) and the observed timing (T^*) is indirectly linked to weather by both pathways. Because success is not a mediator of the relationship between weather and timing, analysing the observed timing could reveal the underlying effects of weather on timing. This figure inferred the simulation previously explained which suggested under this specific struture, there was no bias in only accounting for successful nests.

Figure 3c represents a causal structure where the breeding success is dependent in the breeding timing, which means that in this causal structure, only the successful nests could be considered.

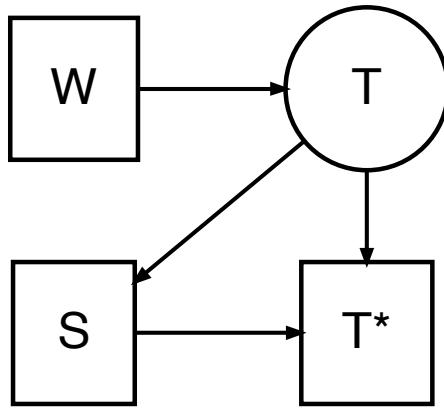


Figure 3c: Directed acyclic graph showing a causal structure between the breeding (T), weather (W), success (S) and observed timing (T^*) under Scenario C.

In Figure 3c, the breeding timing directly influences breeding success in addition to the weather variable of interest, affecting timing. Thus, it is plausible that the effect of the weather variable of interest, on the observed timing, could be due to the direct effects that the weather variable has on breeding timing or through success acting as a mediator. It is reasonable to expect that breeding timing influences success as several studies have found breeding earlier or later in a breeding season, could influence the breeding success (Wingfield 1984; Dunn and Winkler 2019; Reséndiz-Infante and Gauthier 2020). While it is plausible that the breeding timing could influence the breeding outcome within a single breeding season, this scenario is not necessarily true for breeding timing and success at an interannual scale considered in this study.

In the causal structure in 3b, the effect of the missingness depends on what the assumed relationship is between weather, breeding success and timing. If a linear relationship can we assumes between weather and timing, and between weather and success, the estimated relationship between the weather variable of interest and the observed timing is an unbiased estimate of the effects of weather on breeding timing. To see if this is a valid assumption to make, a simulation was conducted to represent the scenario in Figure 3b. Simulation indicated that fitting the models to the observed timing only provided a reasonable estimate for the effects of weather variables on the breeding timing. However, this does not rule out bias under alternative causal structures such as Figure 3c where the breeding success depends on breeding timing, causing only a portion of all nests, to be observed.

6 Results

Here, the results of the analyses determining the effects of weather on the number of active nests, success, and timing of successful nests, of white-backed vultures are presented. The results are structured by objectives, with each based on model selection using an information-theoretic framework. Supporting information and analyses are provided in the appendix.

6.1 Objective 1: Number of Active Nests

The number of active nests shows clear fluctuations across the years, however, there was a clear increase in number of nests over the years of the study (Figure 4).

The number of active nests has increased from fewer than 50 nests per breeding season in the early years of sampling to 138 nests recorded for the 2024 breeding season. Despite the general increasing trend, there were a few years that deviated substantially from the general trend, such as 2009, when the number of active nests dropped from 90 active nests in 2008 to 57 active nests

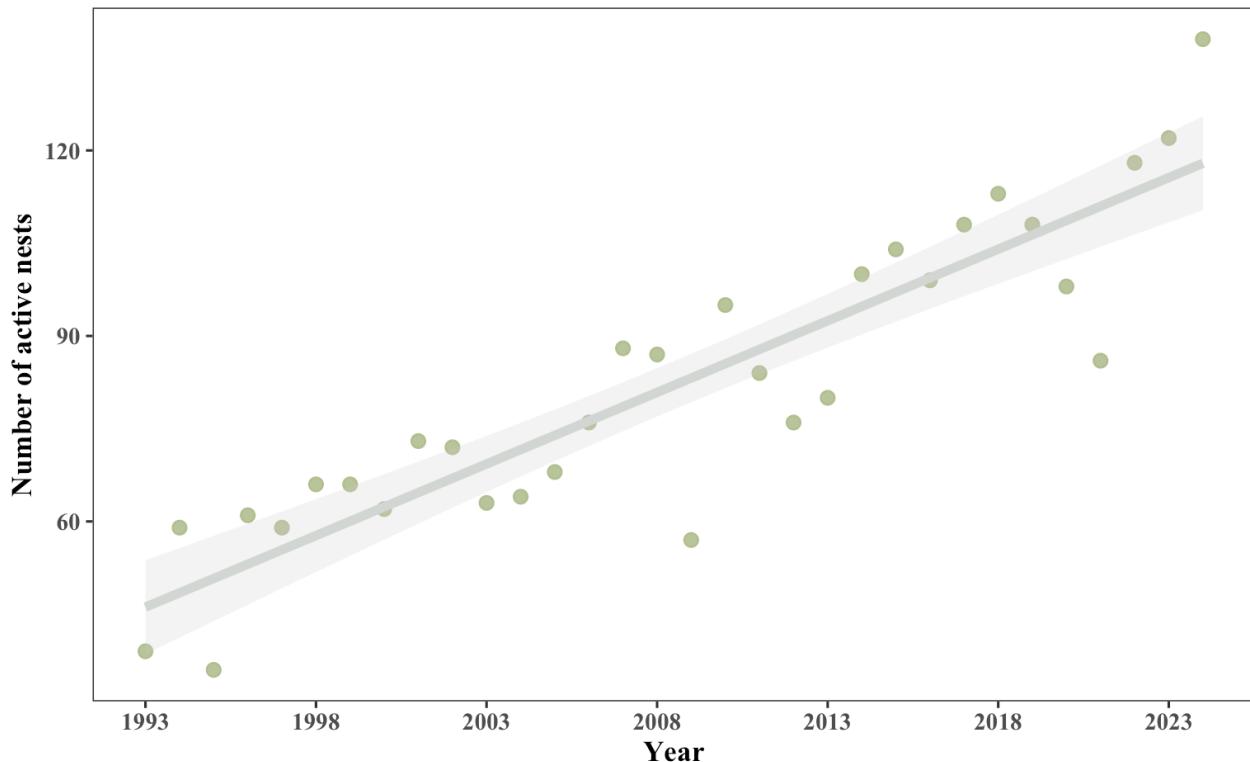


Figure 4: The number of active nests recorded for each white-backed vulture breeding season across the study

period at Dronfield, Kimberely. The grey line represents the best-fitting linear regression line according to the model “Year” in Table 2.

The strong temporal signal observed in Figure 4 was reflected in the model selection results (Table 2). Year accounted for the majority of the variation in the number of active nests, with the selected weather variables accounting for minimal additional explanatory power.

Table 2: The model selection results relating to annual weather variation and the number of active nests at Dronfield (1993-2024) for models including a linear year effect. Models were fitted using linear regressions. A ‘+’ indicates additive effects and ‘ \times ’ indicates an interaction. K is the number of parameters which includes the residual standard error, AICc is Akaike’s Information Criterion; ΔAICc is relative to the best model within this model set; w is the Akaike weight; R^2 is variance explained. Slopes (SE) are reported for simple predictor models only.

Model	K	Deviance	AICc	ΔAICc	w	R^2	slope (SE)
Baseline							
Year (baseline)	3	-35.32	-28.43	0.64	0.14	0.767	
Rain							
Maximum daily rainfall	4	-38.61	-29.07	0.00	0.193	0.790	-0.002 (0.001)
Total rainfall	4	-37.03	-27.49	1.58	0.088	0.779	0 (0)
Previous year’s total rainfall	4	-35.35	-25.81	3.27	0.038	0.767	0 (0)
Rainy days	4	-35.32	-25.78	3.29	0.037	0.767	0 (0.002)
Temperature							
Minimum temperature	4	-36.22	-26.68	2.39	0.058	0.774	0.016 (0.017)
Mean temperature	4	-36.13	-26.59	2.48	0.056	0.773	0.026 (0.030)
Maximum temperature	4	-35.96	-26.42	2.65	0.051	0.772	0.010 (0.013)
Wind							
Maximum wind speed	4	-35.43	-25.90	3.18	0.039	0.768	-0.002 (0.006)
Mean wind speed	4	-35.41	-25.87	3.21	0.039	0.768	-0.019 (0.070)
Hail							
Hail days	4	-35.42	-25.88	3.19	0.039	0.768	0.006 (0.020)
Joint effects							
Min temperature + max daily rainfall	5	-39.84	-27.44	1.63	0.085	0.799	
Max daily rainfall + max wind speed	5	-38.81	-26.41	2.66	0.051	0.792	
Min temperature + total rainfall	5	-37.44	-25.04	4.03	0.026	0.782	
Min temperature + max wind speed	5	-36.23	-23.83	5.24	0.014	0.774	
Max temperature + rainy days	5	-36.18	-23.78	5.29	0.014	0.773	
Hail days + max wind speed	5	-35.52	-23.12	5.95	0.010	0.768	
Hail days + rainy days	5	-35.43	-23.03	6.04	0.009	0.768	

Model	K	Deviance	AICc	Δ AICc	w	R^2	slope (SE)
Interactions							
Prev. rainfall \times max temperature	6	-36.86	-21.36	7.71	0.004	0.778	
Min temperature \times mean wind speed	6	-36.80	-21.30	7.77	0.004	0.778	
Min temperature \times rainy days	6	-36.54	-21.04	8.03	0.003	0.776	

Table 3: Model selection results relating to annual weather variation and the number of active nests at Dronfield (1993-2024) for models excluding a linear year effect. Models were fitted using linear regressions. A ‘+’ indicates additive effects and ‘ \times ’ indicates an interaction. K is the number of parameters which includes the residual standard error, AICc is Akaike’s Information Criterion; Δ AICc is relative to the best model within this model set; w is the Akaike weight; R^2 is variance explained. Slopes (SE) are reported for simple predictor models only.

Model	K	Deviance	AICc	Δ AICc	w	R^2	slope (SE)
Baseline							
Intercept only	2	9.83	14.26	2.22	0.057	0	
Rain							
Maximum daily rainfall	3	8.85	15.74	3.70	0.027	0.031	-0.003 (0.003)
Total rainfall	3	5.94	12.83	0.79	0.117	0.118	-0.001 (0)
Previous year’s total rainfall	3	8.18	15.07	3.03	0.038	0.052	0 (0)
Rainy days	3	9.83	16.72	4.68	0.017	0	0 (0.003)
Temperature							
Minimum temperature	3	9.73	16.61	4.58	0.018	0.003	0.011 (0.036)
Mean temperature	3	9.57	16.46	4.42	0.019	0.008	0.031 (0.062)
Maximum temperature	3	5.88	12.77	0.74	0.120	0.120	0.046 (0.023)
Wind							
Maximum wind speed	3	7.50	14.39	2.35	0.054	0.073	-0.016 (0.011)
Mean wind speed	3	7.96	14.84	2.81	0.043	0.059	-0.18 (0.134)
Hail							
Hail days	3	5.15	12.04	0	0.174	0.140	0.076 (0.035)
Joint effects							
Min temperature + max daily rainfall	4	8.70	18.24	6.20	0.008	0.036	

Model	K	Deviance	AICc	ΔAICc	w	R^2	slope (SE)
Max daily rainfall + max wind speed	4	6.31	15.84	3.81	0.026	0.108	
Min temperature + total rainfall	4	5.91	15.45	3.41	0.032	0.119	
Min temperature + max wind speed	4	7.50	17.03	5.00	0.014	0.073	
Max temperature + rainy days	4	4.83	14.37	2.33	0.054	0.149	
Hail days + max wind speed	4	3.62	13.16	1.12	0.099	0.182	
Hail days + rainy days	4	4.90	14.44	2.40	0.052	0.147	
Interactions							
Prev. rainfall \times max temperature	5	3.31	15.71	3.67	0.028	0.190	
Min temperature \times mean wind speed	5	7.87	20.27	8.23	0.003	0.061	
Min temperature \times rainy days	5	9.55	21.95	9.92	0.001	0.009	

Model selection represented by Table 2 and Table 3, indicated that the number of active nests was weakly associated with weather variables. Models including a linear year trend in Table 2 corresponds with the causal structure represented by Figure 2a, where year is treated as a confounder and should be accounted for. Models excluding the year trend (Table 3) corresponds with the causal structures represented by Figure 2b and 2c. Under these scenarios, time was not a confounder and is not included in the model

The single predictor model including maximum daily rainfall was best supported among models including the year effect ($\Delta\text{AICc} = 0.00$, $w = 0.19$). The year-only model (baseline model) was comparably supported. The baseline model that included only year showed similar support compared to the top-supported model ($\Delta\text{AICc} = 0.64$, $w = 0.14$). The number of rain days and the lagged rainfall (based on the previous year's rainfall) showed limited support ($\Delta\text{AICc} > 2$). Models that included temperature predictors indicated moderate support, with all predictor variables ranging within $\Delta\text{AICc} = 2.3$ and 2.7 . Single models, including wind and hail, showed poor performance. Neither the interaction effect nor the additive models improved the model fit compared to single predictor models, with interactive models received little support ($\Delta\text{AICc} > 7$). Models excluding year (Table 3) addressed an alternative causal structure where the long-term temporal trends do not confound the relationship between weather and the number of active nests. In this scenario, the support for weather variables were still weak, with increasing model complexity, not improving explanatory power. Single predictor models performed similarly to the additive and interactive models ($\Delta\text{AICc} > 7$). When the effect of year was removed, the effect of maximum daily rainfall remained similar, but became uncertain while some

other predictors including hail days and total rain became more important, however, none of the variables explained a substantial part of the variance. Additionally, including weather covariates did not substantially increase R^2 , which indicated that none of these variables explained a notable proportion of variance in the number of active nests.

6.2 Objective 2: Breeding success

The proportion of successful nests decreased with the increasing of number of active nests at Dronfield.

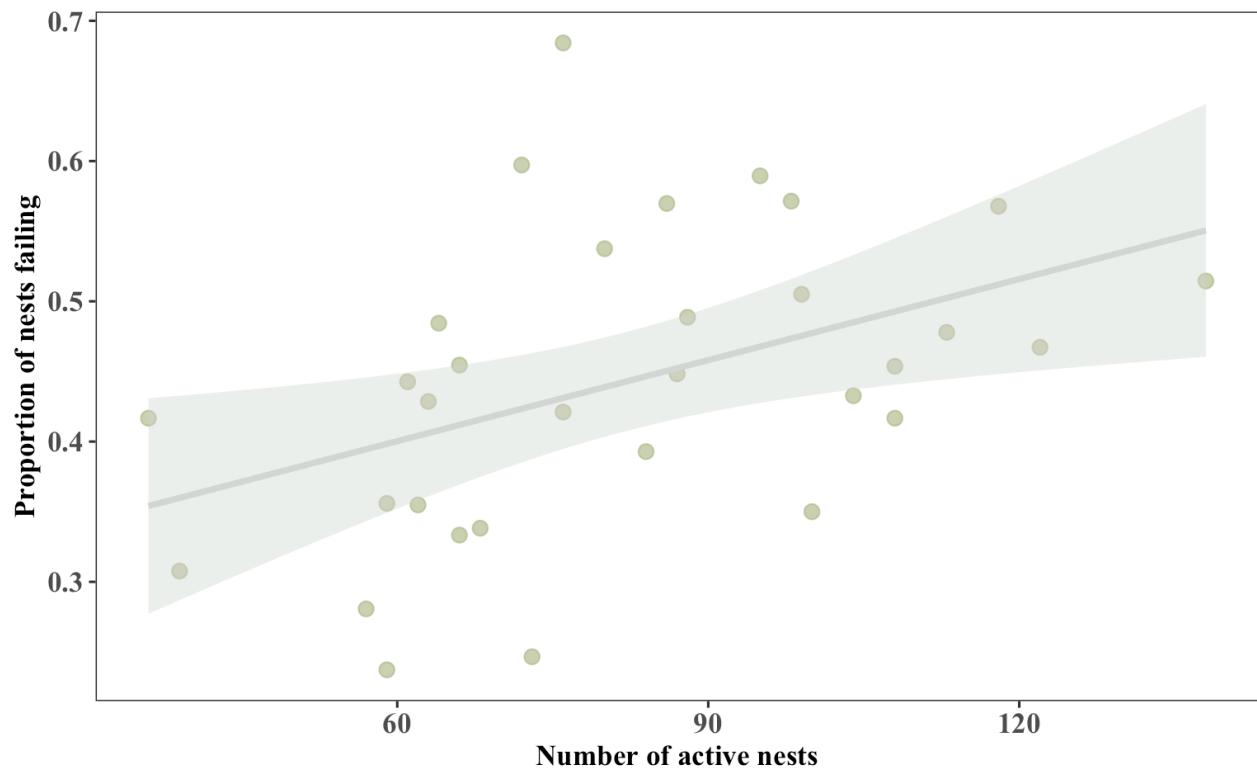


Figure 5: The relationship between the proportion of successful nests and the number of active nest at Dronfield Nature Reserve, Kimberley.

Table 4: The model selection results relating weather predictor variables to breeding success at Dronfield (1993-2024). The models were fitted using generalised linear mixed effects models with year as a random effect, assuming a binomial response and logit link function. A ‘+’ indicates additive effects and ‘ \times ’ indicates an interaction. K is the number of parameters which includes the residual standard error, AICc is Akaike’s Information Criterion; ΔAICc is relative to the best model within this model set; w is the Akaike weight. Between-year variance explained is the reduction in between-year variation compared to the null model. Slopes are represented on the logit scale.

Model	K	Deviance	AICc	ΔAICc	w	Between-year variance explained	slope (SE)
Baseline							
Intercept only	2	225.04	229.45	2.52	0.123	0.000	
Temperature							
Minimum temperature	3	220.07	226.93	0.00	0.435	0.210	0.167 (0.072)
Maximum temperature	3	223.99	230.85	3.92	0.061	0.042	-0.077 (0.075)
Rain							
Maximum daily rainfall	3	224.16	231.01	4.09	0.056	0.034	0.075 (0.079)
Rainy days	3	224.75	231.61	4.68	0.042	0.014	-0.041 (0.076)
Total rainfall	3	224.79	231.65	4.72	0.041	0.008	0.038 (0.076)
Wind							
Maximum wind speed	3	224.88	231.73	4.81	0.039	0.003	-0.031 (0.077)
Hail							
Hail days	3	223.60	230.45	3.53	0.074	0.052	-0.088 (0.073)
Joint effects							
Max temperature + rainy days	4	222.62	232.10	5.18	0.033	0.104	
Rainy days + hail days	4	222.82	232.30	5.38	0.030	0.087	
Hail days + max wind speed	4	223.18	232.67	5.74	0.025	0.062	
Interactions							
Min temperature \times max wind speed	5	219.73	232.04	5.11	0.034	0.225	
Max temperature \times rainy days	5	222.62	234.93	8.01	0.008	0.104	

A posteriori models: population

size

Model	K	Deviance	AICc	Δ AICc	w	Between-year variance explained	slope (SE)
Minimum temperature + number of active nests	4	210.53	220.02	0.00	0.938	0.502	
Number of active nests	3	218.60	225.45	5.44	0.062	0.244	-0.186 (0.071)

The model selection indicated that the breeding success had clearer associations with the weather variables included in the models (Table 4). The model showing the best support (Δ AICc = 0.00, w = 0.44) is the single predictor model including minimum temperature, explaining the largest proportion of temporal variance compared to any of the other models (21%). The other models with single predictor variables explained little extra temporal variance and weak support relative to the best supported model (Δ AICc > 3). The same was seen for models that had additive and interactive predictor variables, showing weak support compared to the best-supported model.

Population size (measured as the number of active nests) was not included in the original model set, which focused on the associations between weather variation and breeding success, however, during the model evaluation, population size was considered an important covariate that might influence breeding success. Population size models were therefore fit as a posteriori analysis. When accounting for population size in the best supported single predictor model, the combined model (minimum temperature + population size) was strongly supported (Δ AICc = 0, w = 0.45) and accounts for 50% of the between-year variation in the breeding success at Dronfield. Minimum temperature was still positively associated with the breeding success in the combined model (Slope = 0.192), and explained 21% of the annual variation in breeding success, in both scenarios. Population size alone showed a negative association with the breeding success (Slope = - 0.186).

Figure 6, showing the relationship between the predictor variable, minimum temperature and breeding success, indicates a positive relationship (slope = 0.167). Years with warmer temperatures had higher breeding success, as the upward trend suggests (Figure 6). The graphs also indicated that the observed breeding success varies substantially around the fitted relationship.

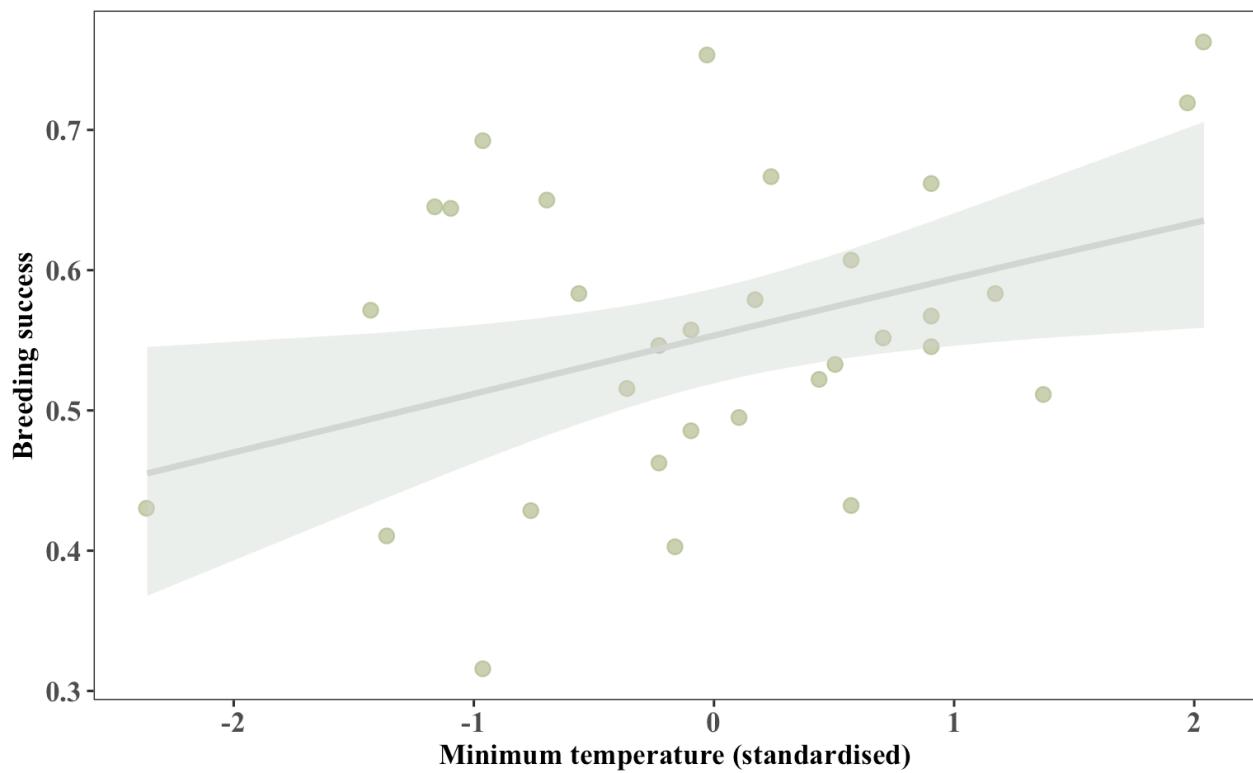


Figure 6: The relationship between minimum temperature and breeding success, expressed as the proportion of active nests that were successful. The grey line represents the best-fitting linear regression line according to the model “Year” in Table 4.

6.3 Objective 3: Breeding timing of successful nests

The breeding timing of successful nests indicated the strongest association with the annual rainfall of the previous year (Table 5).

Table 5: The model selection results for the breeding timing using 30-day pre-laying cues and lagged weather effects from the previous year at Dronfield (1993-2025). The models were fitted using linear regression models. A + indicates additive effects and \times indicates an interaction. K is the number of parameters. AICc is Akaike's Information Criterion; ΔAICc is relative to the best model within this model set; w is the Akaike weight. Between-year variance explained is the reduction in between-year variation compared to the null model.

Model	K	Deviance	AICc	ΔAICc	w	R^2	slope (SE)
Baseline							
Intercept only	2	173.68	178.10	4.58	0.036	0.000	
Temperature (March)							
Minimum temperature	3	171.20	178.06	4.54	0.037	0.075	0.441 (0.284)
Mean temperature	3	171.64	178.49	4.97	0.030	0.062	0.616 (0.437)
Rain (March)							
Rainy days	3	172.75	179.61	6.09	0.017	0.029	-0.143 (0.152)
Total rainfall	3	173.24	180.10	6.58	0.013	0.014	-0.011 (0.018)
Wind (March)							
Mean wind speed	3	171.16	178.02	4.50	0.038	0.076	1.307 (0.833)
Lagged effects (previous year)							
Previous year total rainfall	3	166.66	173.52	0.00	0.356	0.197	0.011 (0.004)
Previous year rainy days	3	172.91	179.77	6.25	0.016	0.024	0.035 (0.040)
Previous year mean temperature	3	173.15	180.01	6.49	0.014	0.016	-0.564 (0.798)
Joint effects							
Previous year rainfall + March rainy days	4	164.90	174.38	0.86	0.232	0.240	
March cues + previous year rainfall	5	163.51	175.82	2.30	0.113	0.272	
Interactive effects							

Model	K	Deviance	AICc	Δ AICc	w	R^2	slope (SE)
Lag rainfall \times March mean temperature	5	163.90	176.21	2.69	0.093	0.263	
Mean temperature \times rainy days (March)	5	169.56	181.87	8.35	0.005	0.121	

Table 6: The model selection results for a posteriori models including population size and the effects of the lagged rainfall on the breeding timing at Dronfield (1993-2025). Models were fitted using linear regressions. A ‘+’ indicates additive effects and ‘ \times ’ indicates an interaction. K is the number of parameters. AICc is Akaike’s Information Criterion; ΔAICc is relative to the best model within this model set; w is the Akaike weight. Between-year variance explained is the reduction in between-year variation compared to the null model.

Model	K	Deviance	AICc	ΔAICc	w	R^2	slope (SE)
Population size models							
Previous year rainfall + number of active nests	4	161.33	170.81	0.00	0.722	0.320	
Previous year total rainfall	3	166.66	173.52	2.71	0.186	0.197	0.011 (0.004)
Number of active nests	3	168.09	174.95	4.14	0.091	0.160	-1.485 (0.621)

The breeding timing at Dronfield was best explained by the total annual rainfall of the previous year (Table 5), with this model receiving the strongest support among the other weather models ($\Delta\text{AICc} = 0.00$, $w = 0.356$). Additionally, this best supported model accounted for 19.7% of the between-year variation in laying date. The other lagged models received less support and added little explanatory power to the between-year variation in laying date. Models that included weather variables representing the weather conditions in March (approximately one month before breeding starts), indicated weaker support ($\Delta\text{AICc} > 4.5$) and explained substantially less between-year variation compared to rainfall from the previous year. Models where variables were combined with the lagged rainfall added moderate explanatory power compared to the power of the best fit model. Models including both rainfall variables (lagged rainfall and number of rainy days) added the most explanatory power between the combined models ($\Delta\text{AICc} = 0.86$, $w = 0.232$) but support remained lower than the single lagged rainfall model.

Because of laying dates only observed for the successful nests, whether these results could be applied to all nests, depends on the causal structure. If the DAG in Figure 3a is plausible, which suggests breeding success is random in terms of the weather variables used to explain variation in breeding timing, then estimates derived from the successful nests, can be applied across all nests. Under the scenario depicted by Figure 3b, success depends on breeding timing, but not directly on the weather variable of interest, the simulated results suggest that excluding the unsuccessful nests does not create bias and thus, the results can be applied for all nests.

If breeding timing directly influences the breeding success as seen under causal structure in Figure 3c, the

observed timing of successful nests represents only a subset of all nests, which means the observed effects of the weather variable of interest, on the observed timing is confounded by which nests succeed. Inference is therefore restricted to successful nests only.

In Figure 3d, a unobserved variable, acting as a confounder, influences both breeding timing and breeding success. Including the number of active nests, as a proxy for population size in the models helped control for one plausible candidate that effects that had influence on both breeding success, and timing. When the number of active nests (a proxy for population size) was included in the posterior models, the model became the best supported model ($\Delta AIC_c = 0.00$, $w = 0.722$). Additionally, adding the number of active nests to the lagged rainfall model, added an increase to the explanatory power, increasing to 32%. Consistent with this scenario in Figure 3d, models including the number of active nests accounts for population-level effects on both breeding timing and breeding success, thus, under this structure, the results from models that includes the number of active nests, can be applied to all nests. However, population size is likely to only represent a portion of what node X is in reality, therefore it is important to note that other unmeasured variables such as carrion availability could influence both timing and success.

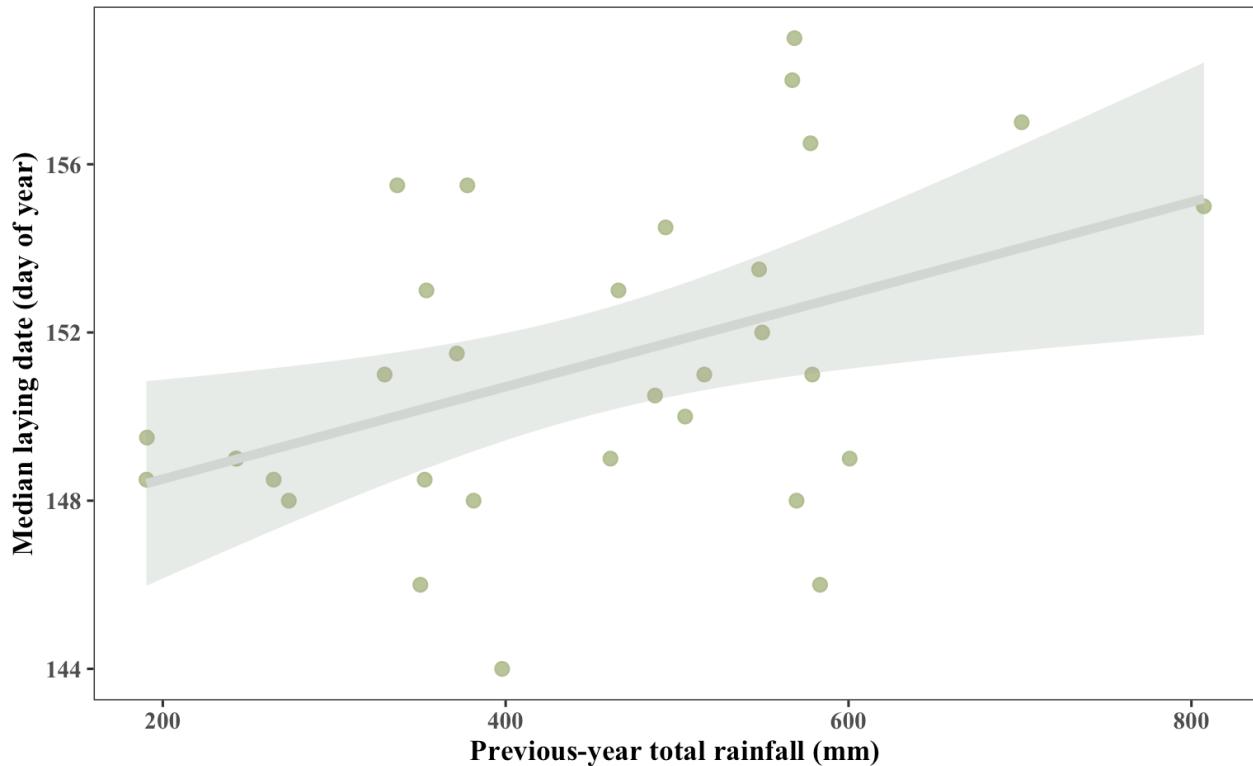


Figure 7: The relationship between the mean laying date, measured day of the year, and total annual rainfall of the previous year (lagged total rainfall), at Dronfield, Kimberley between 1993 and 2025. Each data point

represents a single breeding season. The grey line represents the best-fitting linear regression and the shaded area, the 95% confidence interval.

Figure 7, representing the relationship between the mean laying date and total annual rainfall of the previous year shows that breeding seasons following higher rainfall years, tend to indicate later laying dates. This relationship is indicated by the positive slope of the fitted linear regression line.

7 Discussion

The role of weather variability in shaping avian reproduction is increasingly recognised, with multiple studies showing that weather influences reproduction through several pathways, including increased energetic cost, limiting foraging abilities and through direct exposure of eggs and chicks to unfavourable conditions (Jenouvrier 2013; Sauve et al. 2021; McCloy and Grace 2023; Osborn 2023). This study investigated the effects of inter annual weather variation on three components of the breeding cycle of the critically endangered African white-backed vulture, namely breeding effort, breeding success and breeding timing.

Our results suggest that weather variability influences each stage of the breeding cycle in distinct ways. The number of active nests indicated a long-term increase across the study period, with notable variability between years, with little variation explained by weather variables. Instead, longer-term temporal processes accounted for the majority of the observed variation in the number of active nests. Breeding timing and breeding success indicated a stronger relationship with weather compared to the number of active nests, however, no single weather variable accounted for the majority of the between-year variation. To interpret these patterns, alternative causal relationships between weather, time-trend and the three breeding variables were considered using directed acyclic graphs to align inference with different plausible causal scenarios.

Number of Active nests

The number of active nests increased over time and indicated a clear long-term upward trend in active nest numbers per breeding season, despite yearly fluctuations over the study period. This increasing trends suggests that the at Dronfield, the number of breeding pairs have increased over time, but can also reflect the increasing population size at the reserve, over the study period. The colony of white-backed vultures at Dronfield experienced an estimated 50% increase in colony size between 1993 and 2014 (Murn et al. 2017; Leepile et al. 2020). However, this does not reflect the general trend of declining population sizes across the greater geographical range of white-backed vultures (Murn et al. 2017). Therefore, the trend increasing trend noted

at Dronfield could be attributed to site-specific conditions such as the stable land management and increased food availability over the years, rather than birds migrating to Dronfield from different areas as no tagged birds from different areas have been noted at Dronfield (A. Anthony pers. comm. 2026).

In contrast to what was expected, variation in weather conditions between years explained only a small portion of the variation in the number of active nests compared to the amount of variation accounted for by the temporal structure. This finding suggests that the number of active nests during the breeding season of African White-backed vultures is more likely to be explained by long-term population-level processes, rather than weather variability. Similarly, a previous study conducted by Virani et al. (2012) on the seasonal variation in breeding of Rüppell's vultures in Kenya noted that the number of occupied nests during the breeding season is shaped by the accumulation of long-term effects on the population. The number of nests of both Rüppell's vulture and Lappet-faced vulture populations fluctuated independently of the population size, which suggests breeding participation of these species is more likely linked to individual condition and resource availability (Virani et al. 2012).

Causal structure represented in figure 2b and 2c were initially considered as a plausible scenarios for shaping the number of active nests because some of the weather variables showed long-term trends across the study period and in turn, they could have caused a trend in the number of active nests (See appendix Figure 1A). However, the results indicated that the weather variables assessed, did not explain much variation in the number of active nests between years, regardless of whether the year trend was accounted for, or not.

Our finding is therefore best represented by the confounded causal structure Figure 2a, where the temporal trends, influence both weather and the number of active nests. Year acts as a confounder in the relationship between weather and breeding effort, and associations between the weather and the number of active nests could be caused by the shared temporal structure rather than a direct effect of weather. The temporal trend in the number of active nests is more plausibly linked to possible long-term population-level processes, such as a shift in food abundance over time or a change in the body condition of adult birds (Scopel and Diamond 2018; Nägeli et al. 2022).

Although weather variation explained minimal variation in the number of active nests, it is interesting to note that models excluding year indicate an association between maximum daily rainfall and the number of active nests. While studying how rainfall affects the breeding effort of vultures in Namibia, Bridgeford (2003) found that the relationship between breeding effort and rainfall has an inverse relationship, with wetter years being followed by fewer nests. This relationship has, however, been directly linked to food availability, as drier

conditions increase carcass availability and so, improving the body condition of adult birds for the breeding season (Bridgeford and Bridgeford 2003). Consistent with our results, though, they also noted that rainfall alone does not explain variation in the number of active nests, but the time-trend and population level structures had a stronger influence than rainfall directly.

Initially, we hypothesised that there will be a decline in the number of active nests in years with high temperatures, high wind speeds and prolonged rainfall events, however, our results suggest that weather conditions explained minimal interannual variation in the number of active nests across the study period. Instead, the variation in the number of active nests are explained by the strong temporal trend.

Breeding success

The breeding success of many avian species is strongly influenced by the surrounding environmental conditions, as eggs and nestlings require a specific set of conditions for normal development (Martin et al. 2017). Our results indicated that breeding success had a higher association with weather than breeding effort, which suggests that the breeding outcome is more likely to be shaped by environmental conditions. From the variables assessed, minimum temperature, reflecting overnight or early morning conditions, was the best supported predictor variable for breeding success in a given season, with higher success predicted for years with higher minimum temperatures. The effect, however, was moderate, which means there could be multiple factors interacting together that influence breeding success. Despite its moderate effects, this finding is consistent with research on the effects of low thermal conditions on the breeding success of avian species. During the night, many bird species, including vultures, are not active, meaning no heat is generated through movement during the coldest hours of the day (Elkins 2010; García-Jiménez et al. 2020). Therefore, during these low temperatures, they have to rely on stored energy to maintain optimum body temperature, and chicks are specifically vulnerable during these periods because they are unable to thermoregulate properly (Elkins 2010). In addition, cold winds and low humidity conditions could increase the amount of heat loss by eggs and chicks, as eggs are also susceptible to losing heat quite rapidly (Elkins 2010; Pipoly et al. 2013). Therefore, warmer conditions are often associated with increased breeding success, coinciding with our findings.

Research conducted on the effects of weather conditions on the breeding success of western capercaillie (*Tetrao urogallus*) found that the reproductive output was positively associated with warmer temperatures, with larger brood sizes and higher chick survival rates noted during warmer periods (Coppes et al. 2021). However, they attributed this increase in breeding success through an indirect pathway, which is better general environmental conditions and increased food availability, rather than to the direct effects of temperature on the chicks (Coppes

et al. 2021). Despite temperature representing a biologically plausible predictor for breeding success through different pathways, the moderate effect size, and it being the only predictor variable with notable explanatory power, suggests that breeding success is influenced by more than a single or interacting weather variable. When the number of active nests (a proxy for population size) was incorporated into the minimum temperature model, the model support increased significantly. However, the effect of minimum temperature remained the same in the combined model. Years with a higher number of active nests, had lower numbers of successful nests, which indicated that even in more optimum weather conditions, there might be density-dependent constraints (Carrete et al. 2006; Fernández-Bellon et al. 2016). While studying the effects of density-dependent productivity of the colonial cinereous vulture, the authors found that the breeding success declined with increasing colony density and saturation (Fernández-Bellon et al. 2016). At the Dronfield colony, there is a clear increase in the number of active nests, however, this could increase competition between breeding pairs and the reduction of shared foraging resources, like with the cinereous vulture (Fernández-Bellon et al. 2016). Additionally, because the number of active nests still increases over time at Dronfield, it is possible that numerous other variables with a time trend could influence the breeding outcome. For example, blood-lead toxicity levels of chicks have increased at Dronfield (Van den Heever et al. 2023), which could be attributed to lower success rates in years that are characterised by increased levels of lead poisoning.

The initial hypothesis for the effects of weather conditions on the breeding success expected a decrease in the breeding success in years with higher temperatures, wind speeds, hail days and prolonged rainfall events due to possibly lower reproductive investment. The results suggest that there were certain weather variables that did have a role in shaping breeding success of white-backed vultures at Dronfield, however, contrary to what was hypothesis, higher temperatures were associated with increased breeding success. Though the results do indicate an influential role of weather in shaping the breeding success of white-backed vultures at Dronfield, the strength and direction of these relationships showed variation which suggests that weather conditions are likely to affect the breeding success in conjunction with other population level processes.

Breeding timing of successful nests

The results for the analysis on the effects of weather variables on the breeding timing of successful nests suggests that breeding timing was most strongly associated with the total annual rainfall of the previous year, rather than weather cues during the pre-laying period. Relationships like this are often referred to as lagged effects where conditions experienced in one year, or season, has effects on the demographic rates such as breeding, in the following year (Mainwaring et al. 2021; Zwaan et al. 2022). Hinsley et al. 2016 investigated the effects of weather conditions on the laying date of great tits and found that the laying date within a given

breeding season was predicted by the weather conditions of the previous year through its influence on spring temperatures (Hinsley et al. 2016).

In contrast to lagged effect, a controlled aviary study was conducted on great tits to determine if different weather conditions acts as an immediate cue to initiate breeding, or if they are responding through an indirect cue such as food availability (Visser et al. 2009). Two control groups were used, with one group exposed to a warm treatment and the other to colder temperatures. They found that the birds exposed to warmer conditions laid their eggs approximately six days earlier than birds in the colder control, 4°C cooler (Visser et al. 2009). Additionally, they found that the laying date was most influenced by temperatures experienced three weeks before laying, suggesting these birds use temperature as a cue to initiate laying. Interestingly, our results did not indicate a strong relationship between the pre-laying weather conditions and breeding timing which suggests that the pre-laying conditions are less influential compared to lagged effects.

For white-backed vultures at Dronfield, a different mechanism of lagged effects could be plausible. Dronfield is surrounded by landscape of game farms which is the main food source for the white-backed vultures at the reserve. The positive relationship between the lagged annual rainfall and breeding timing suggests that years with high annual rainfall, are associated with later laying dates. Years with higher rainfall is typically associated with more productive conditions, such as food supply for herbivore populations in the surrounding areas. Herbivore condition and survival is therefore typically improved in high rainfall years, which reduces carcass availability for the vultures. This reduction in food availability could delay breeding in adult birds as they might need more time to reach sufficient body condition before they initiate breeding (Blums et al. 2005). Better body conditions are often associated with earlier breeding in many species (Blums et al. 2005). In mallards (*Anas platyrhynchos*), female birds that had a better body condition, initiated breeding 15 days earlier than females who had below average body conditions (Devries et al. 2008).

By including the number of active nests, a proxy for population size, the model improved and additional between-year variance was explained. This suggests that even in the presence of, for example, density-dependent processes within the population of white-backed vultures at Dronfield, the timing of breeding has stronger associations with the environmental conditions from the previous year affecting food availability and body condition.

In our analyses, because breeding timing was only measured for the successful nests, it should be considered whether these results are representative of all active nests during each breeding season. This raised the possibility of bias in the true changes of breeding timing by only accounting for successful nests. To assess the

possibility of bias, a simulation was conducted under causal structure represented in Figure 3b, where weather influences both breeding timing and success directing, but there is no influence of the laying date, on success. Under this scenario, using only successful nests did not create bias.

This limitation would be most concerning if the timing determined nest success within a breeding season, as depicted under the scenario in Figure 3c. This is because experimental studies suggest that as the breeding season progresses, the breeding success decreases, a pattern that possibly arises because the timing of breeding has a causal effect on breeding success (Verhulst and Nilsson 2008). However, our analyses focused on the variation in laying dates between years, rather than the difference among nests within the same breeding season, and therefore, a change in breeding timing reflects changes in weather conditions between years. At this temporal scale, variation in weather is more likely to affect timing, and success through separate pathways, directly at the population level rather than through how breeding timing, affects the outcome (Both 2010). The relationship between timing and success are often noted to be strong within seasons, however, this relationship can vary over a larger temporal scale, especially when there is notable variation in environmental conditions across the years (Both 2010). This is consistent with results found by Eeva et al. 2000 where they studied breeding timing of four tit species and found that breeding success is not dependent on breeding timing. Breeding timing of these species were rather inferred by conditions relating to good food availability (Eeva et al. 2000). Considering the alternative causal structure in Figure 3d, where the unobserved variable influenced both breeding timing and the breeding success, including the number of active nests as a proxy for population size, aided in controlling for one plausible explanation of what the unobserved variable could be.

By analysing the relationship between breeding timing and weather conditions in the pre-laying period, and lagged weather conditions, our results suggest the contrary to our proposed hypothesis as breeding timing was not strongly associated with the weather conditions in the immediate pre-laying period, 30 day prior to laying date. The results indicate a stronger influence of the lagged weather effects, especially rainfall of the previous year in shaping interannual variability between the laying date across the study period. This suggests that breeding timing of white-backed vultures at Dronfield are influenced by indirect effects of weather on the breeding ecology, by resource limitation.

This study aimed to assess how weather variability affected the three different components of the breeding cycle of African White-backed Vultures. By assessing the number of active nests, breeding success, and the timing of successful nests over the 31 year study period, our results of the affects of weather conditions varied across the three stages of the breeding cycle assessed which, importantly, indicates that weather influences breeding through different pathways. These findings, which highlights the effects of annual climate variability

rather than long-terms shifts in climatic conditions, could aid in predicting how African white-backed vultures may respond under future climate change projections, which could help infer conservation planning and management of this endangered species. For example, the findings for our colony, together with existing literature emphasises the role of food availability in shaping reproduction of many bird species. Thus, under weather conditions that limit foraging ability and food availability, the use of strategic vulture restaurants could be used to mitigate the consequences on breeding. Building on this research, future research should aim for a more complete timing data set with data for both successful and unsuccessful nests to be able to address all plausible scenarios of how timing affected reproductive output. In addition, although it might be challenging to quantify, it would be informative to include a measure of food availability as the effects of weather on carrion availability is a likely mediator between weather and reproduction. Given the continuous decline of African white-backed populations across Africa, understanding how environmental variability is shaping their reproduction is a critical component in understanding how these populations might respond to future climate change scenarios.

A Appendix

The link to GitHub repo, including my full analyses can be found here: <https://github.com/miekedeyzel/VultureProjectR>

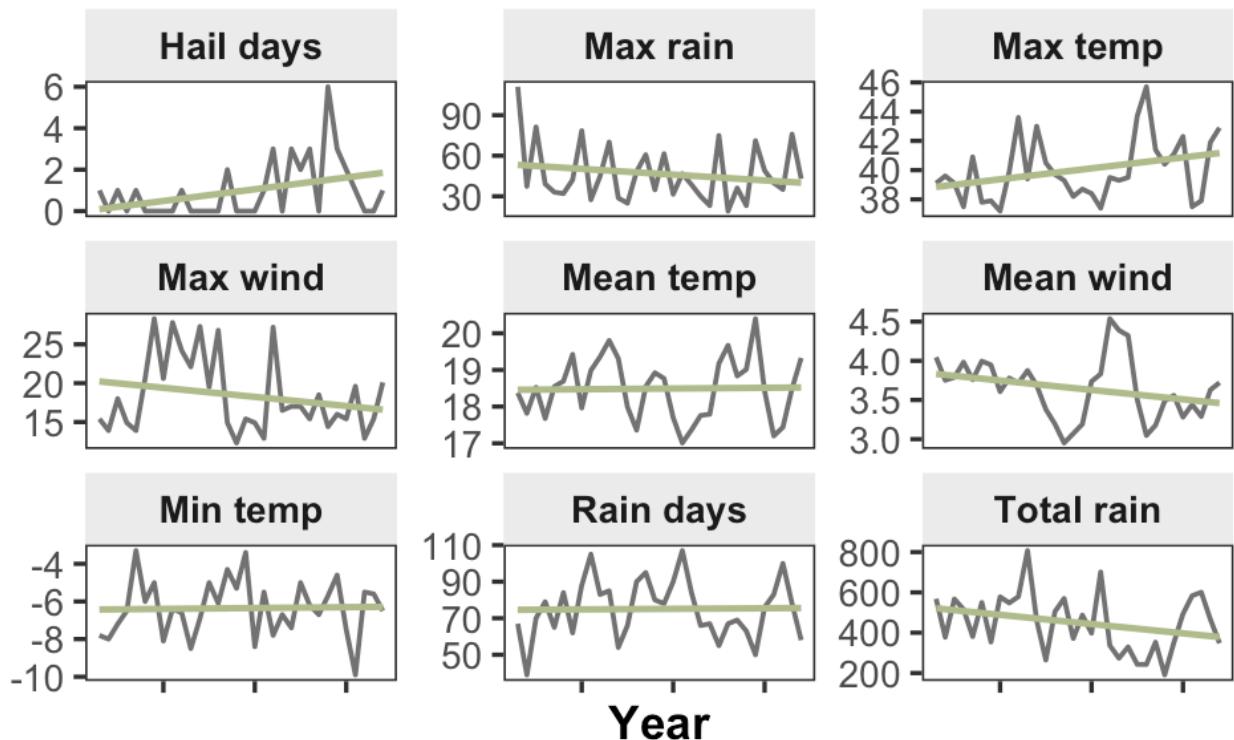


Figure A1: The temporal trends of the weather variables included in the analysis. Data is derived from the Kimberley meteorological station (1993 - 2024). Annual values are represented by the grey lines with the green lines representing the fitted linear trend.

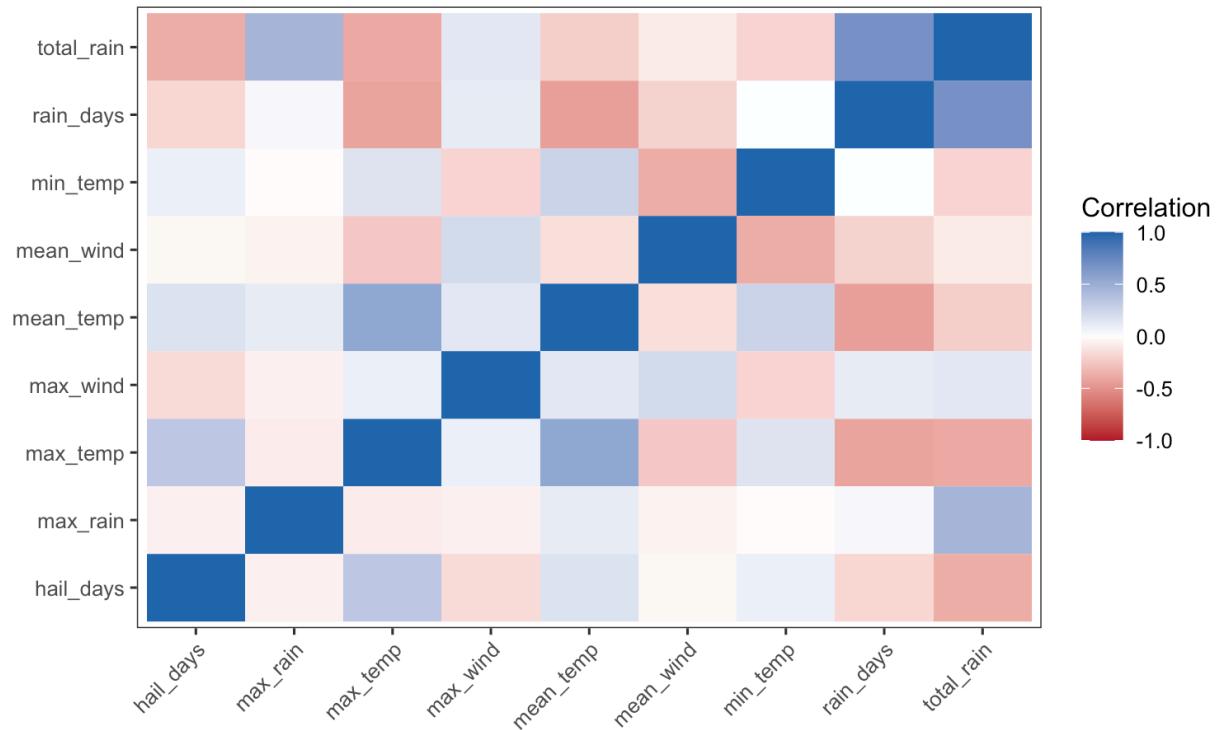


Figure A2: A correlation matrix showing the persons correlation coefficients between all weather variables included in the analyses on the effects of weather on the breeding ecology of African white-backed vultures at Dronfield (1993-2025).

Table A1: Codes used to describe nest and breeding status during field surveys at Dronfield Nature Reserve, Kimberley.

Code	Description
1	Chick ringed.
2	Chick too small to ring.
3	Chick too big to ring.
4	Chick fledged.
5	Nest new lining (for this breeding season).
6	Nest egg shell fragments (for this breeding season).
8	Nest with white wash.
10	Nest inactive.
11	Nest collapsed.
13	Nest gone.
14	Other bird species nesting.
15	Egg (for this breeding season).
16	Nest rebuilt, lined with dead chick, bones or feathers (for this breeding season).
17	Nest rebuilt, not lined (for this breeding season).
18	Nest under construction (for this breeding season).
19	Found in August, not checked in October.
20	Found in October, not seen in August.
–	Nest tree, used for the first time this year.
–	Pylon nest.

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