

The Effects of Climate Change on the Breeding Success and Timing of African White-backed Vultures

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Table of contents

1 Abstract	2
2 Introduction	2
2.1 Aims and Objectives	6
3 Methods	7
3.1 Study Area	7
3.2 Data collection	8
3.2.1 Field data collection	8
3.3 Data Analyses	9
3.3.1 Weather data	10
3.3.2 Statistical analyses	10
3.3.3 Directed acyclic graphs (DAGs)	11
4 Results	15
4.1 Objective 1: Number of Active Nests	15
4.2 Objective 2: Breeding success	20
4.3 Objective 3: Breeding timing of successful nests	22
5 Discussion	24
6 Conclusion	26
7 Appendix	26
Bibliography	26

1 Abstract

2 Introduction

Climate change is widely projected to alter ecological systems by increasing the variability in weather patterns and the frequency of extreme events across the globe (Abbass et al. 2022). Events such as severe droughts, heat stress and flooding are predicted to become more frequent, leading to significant pressure on ecological systems. As climate change continues to be a growing concern, many studies have focused on determining how climate change is affecting the mean climatic conditions of environmental systems (Thornton et al. 2014). Consequently, fewer studies have focused on how increasing smaller scale weather variability may be a major driver of ecological disruptions, despite evidence suggesting the influential role of inter annual variation on ecological responses (Thornton et al. 2014; Maxwell et al. 2019).

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. 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 in the future (Maclean and Wilson 2021; Cockrem 2022).

Most organisms have optimal temperature ranges and preferences for the amount, and timing of precipitation and as weather conditions move away from the optimum, it often leads to consequences for the species distribution, growth, reproductive success and survival. Climate change and variability alters key environmental cues by shifting rainfall and temperature regimes which could cause significant disruptions to the geographical distribution, growth, reproduction, migration, survival and other important processes of many species (Inouye 2022). In the event of increasing temperatures, for example, important processes such as the reproductive timing and migration, has noted to be advanced. Although these phenological shifts could help animals adapt to the changing environment, however, this often causes other ecological processes or food availability to fall out of sync, which could reduce the fitness and reproduction of individuals (Inouye 2022).

Alongside many other animal species, avian populations are particularly sensitive to unpredictable variation in climatic conditions as they heavily rely on specific environmental conditions to regulate important life-history process such as reproduction, migration and foraging efficiency. Thus, global climate change and its resulting conditions such as altered temperature and rainfall regimes and more frequent extreme events could both directly and indirectly have an effect on avian populations during any life-history process (Cockrem 2022). The study of how weather patterns are effecting avian population biology has become a growing field of study over the years, with particular emphasis on the effects of weather conditions on the breeding ecology of many bird species (Jenouvrier 2013; Sauve et al. 2021; Osborn 2023). Weather conditions are able to 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).

Reproduction is in itself, is one of the most energetically demanding life-history staged 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 compensation, 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 parental birds to change their breeding strategies by choosing not to breed during the season entirely, changing their breeding timing, 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 should not go unmentioned. 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). Thus, possibly leading to reduced investment in parental care and therefore reducing 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, as their thermoregulatory ability is underdeveloped (Kosicki 2012). Additionally, in more severe instances, prolonged periods of rain-

fall could cause nest flooding, often causing nest collapse or the drowning of chicks (Ortega et al. 2022) Thus, conditions deviating from the optimum for chick survival, could significantly reduce the breeding success of avian populations. A study conducted on the relationship between reproductive success weather conditions of Kestrels found that in the event of inclement weather, there were significant impacts of the reproductive success. During these unfavorable 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 suggest 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 well-known that temperature influences breeding timing with warmer temperatures often shifting egg-laying earlier in the breeding season through behavioral responses to warming conditions. 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 parental birds, may differ to the last due to the different conditions they might have experienced earlier in the year, affecting their body condition. If adult birds are experiencing decreased body condition, they are more inclined to delay breeding, or will not initiate breeding entirely for this breeding season (Zwaan et al. 2022). Alongside reduced body condition, more frequent, or prolonged storm events often leads 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 foraging efficiency of many bird species, particularly those who use thermals for their flight, like vultures. In contrast, rainfall events often signals 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).

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

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, including 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 [van2020integrating]. 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). 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 in southern Africa (Mundy et al. 1992). White-backed vultures are monogamous, and during breeding season, one egg is laid typically between April – July. Thereafter, the egg is expected to hatch after roughly 60 days, which is 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%.

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. In the context of vultures, it has been proposed that climate change could have

contributed to the historical loss of Cape vulture colonies, resulting from increased temperatures and shifts in rainfall patterns documented in the region (Phipps et al. 2013). Cape vultures nest at high elevations, typically on the edges of cliffs, making them and their nests sensitive to weather extremes such as prolonged periods of sun exposure that cause heat stress, decreasing the overall breeding success of the colonies (Phipps et al. 2013).

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.

2.1 Aims and Objectives

This study aims to assess how inter annual weather variation influenced the breeding cycle 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 inclement 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 inclement 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 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 effecting 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.

3 Methods

3.1 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 found across the reserve. This breeding colony is one of six in the greater Kimberley area, with few 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, such as lead poisoning associated with hunting activities and drowning in surrounding farmland areas while foraging. 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.

3.2 Data collection

3.2.1 Field data collection

The long-term monitoring program of African White-backed vultures commenced in 1993, with few methodical 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 end of 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. 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 capture any new nests that might have been established and to limit the possibility of double-counting nests. 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.

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, was 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. Each nest identified during the first survey in August was revisited and assessed for its breeding outcome. For a nest to be classified and 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. Wing length was used as a proxy for chick age, as it is a consistent metric for estimating the relative age during early development. 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.

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.

3.3 Data Analyses

We 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, we 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). All statistical analyses were conducted in R statistical computing environment (R version 4.4.1).

3.3.1 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 (Posit Team 2025). The weather variables were derived from 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, rainfall, temperature and extreme events were assessed for their impacts on the three outlined focus areas of the breeding cycle. Using the daily weather summaries derived from the weather station, annual and seasonal summaries were used to generate the weather predictors used in the analysis.

3.3.2 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. Therefore, each model was representative of an explanation for the observed variation in the number of active nests, breeding success and timing.

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. 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, measured as the number of active nests in each breeding season, was log-transformed before conducting the analyses to adhere to model assumptions, whereas breeding timing was deemed normally distributed before fitting the model. The breeding success objective was analysed using binomial models using a logit link function, as breeding success

is measured as the proportion of successful nests relative to the total number of nests each breeding season. By using the proportion of successful nests, it accounted for the variation in sample sizes across the multiple breeding seasons.

Due to the temporal structure of the data, year was added to the analyses to account for the unmeasured annual variation that is not directly attributed to weather conditions. For the number of active nests, models were fitted with and without year as a covariate to compare models and determine the effects of weather conditions with and without accounting for the temporal trend. In the breeding success models, year was added to the models as a random effect to account for the unmeasured annual variation in the baseline breeding success, while the fixed effects of weather were modelled. 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 on the pre-laying period, weather variables were summarised for the 30 and 60 days before the laying date and fitted to the models.

The laying date was only available for the successful nests, as the unsuccessful nests lacked the information needed to estimate laying date. To see whether the missing data created bias in the model, a simulation was conducted on the causal structure where weather influenced both laying date and breeding success, and laying dates were only recorded for successful nests. After fitting the model to the simulation, the data estimated effects of weather matched the true effect. Therefore, despite the missing date, using only the laying date of successful nests provided a reasonable estimate for the effects of weather variables on the breeding timing.

3.3.3 Directed acyclic graphs (DAGs)

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.

Number of Active Nests

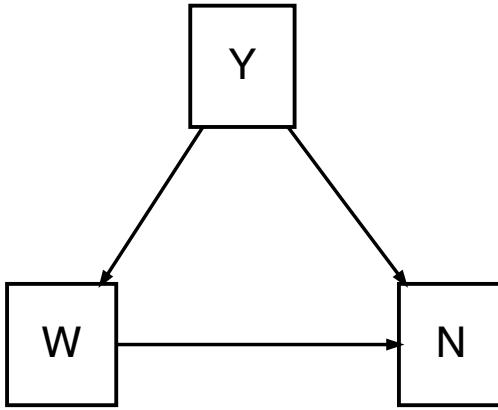


Figure 1a: Directed acyclic graph showing a confounded causal structure between the number of active nests (N), year (Y), and weather (W).

In Figure 1a, 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.

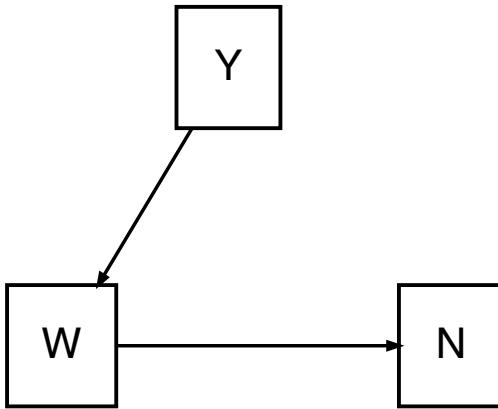


Figure 1b: Directed acyclic graph showing a causal structure the numver of active nests (N), year (Y) and weather (W).

In Figure 1b, the scenario represented how the temporal structure (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.

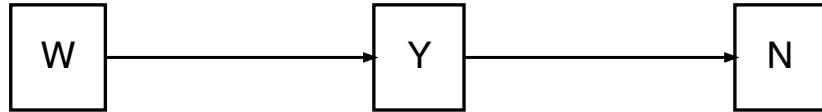


Figure 1c: Directed acyclic graph showing a mediated causal structure between the number of active nests (N), year (Y), and weather (W).

In Figure 1c, the scenario represented how the temporal structure (Y) acted as a mediator of the weather effects on the number of active nests, where weather influenced year and in turn, 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 a part of the effects of interest. Therefore, to estimate the total effects of weather on the number of active nests, year should'nt be included as a control.

Breeding timing of succesfull nests

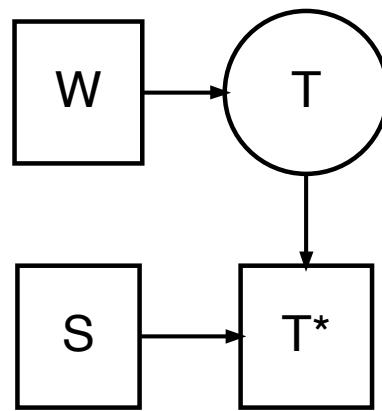


Figure 2a: Directed acyclic graph showing a mediated causal structure between the breeding timing of successful nests, weather (W), success (S) and observed timing (T^*) under scenario A.

In Figure 2a, weather did not affect the breeding success of successful nests, meaning success is random with respect to the weather variable used to explain breeding timing. Therefore, success does not act as a confounder

in this scenario and analysing the observed timing (T^*) yields the correct inference about the effect of weather on timing.

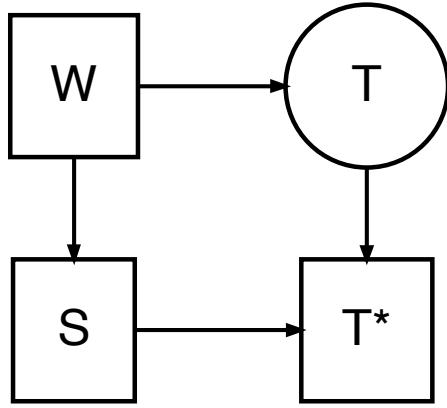


Figure 2b: Directed acyclic graph showing a causal structure between the breeding timing of successful nests, weather (W), success (S) and observed timing (T^*) under Scenario B.

In Figure 2b, 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.

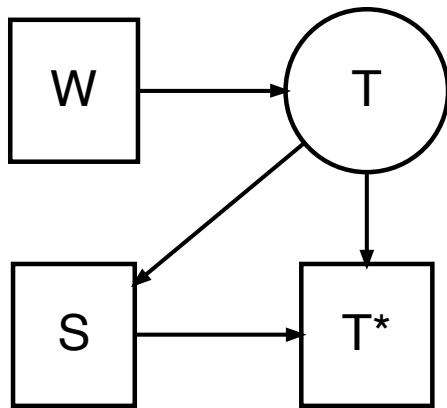


Figure 2c: Directed acyclic graph showing a causal structure between the breeding timing of successful nests, weather (W), success (S) and observed timing (T^*) under Scenario C.

In Figure 2c, breeding timing directly influenced breeding success, in addition to weather affecting timing. In this scenario, it is not clear if the effects of weather (W) on the observed timing (T^*) is a direct causal effect on breeding timing or mediated through success. This scenario becomes less clear in an between-year scale because breeding earlier or later within a season is not necessarily linked to higher breeding success.

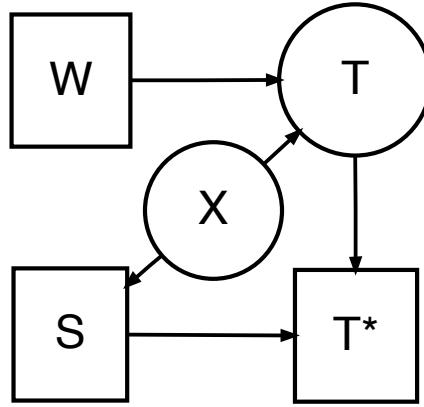


Figure 2d: Directed acyclic graph showing a causal structure between the breeding timing of successful nests, weather (W), success (S) and observed timing (T^*) and population size (X) in Scenario D.

In Figure 2d, an unobserved variable (X), population size, influences both breeding timing of successful nests (T) and the breeding success (S). Because population size effects both timing of successful nests and breeding success, it acted as a confounder and the way in which weather effects the observed timing (T^*) cannot be identified without accounting for the shared influence,

4 Results

In this chapter, the results of the analyses determining the effects of weather on the number of active nests, success, and outcome 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.

4.1 Objective 1: Number of Active Nests

The number of active nests shows clear fluctuations across the years, however, the long-term increase in number of active nests remains evident (Figure 8).

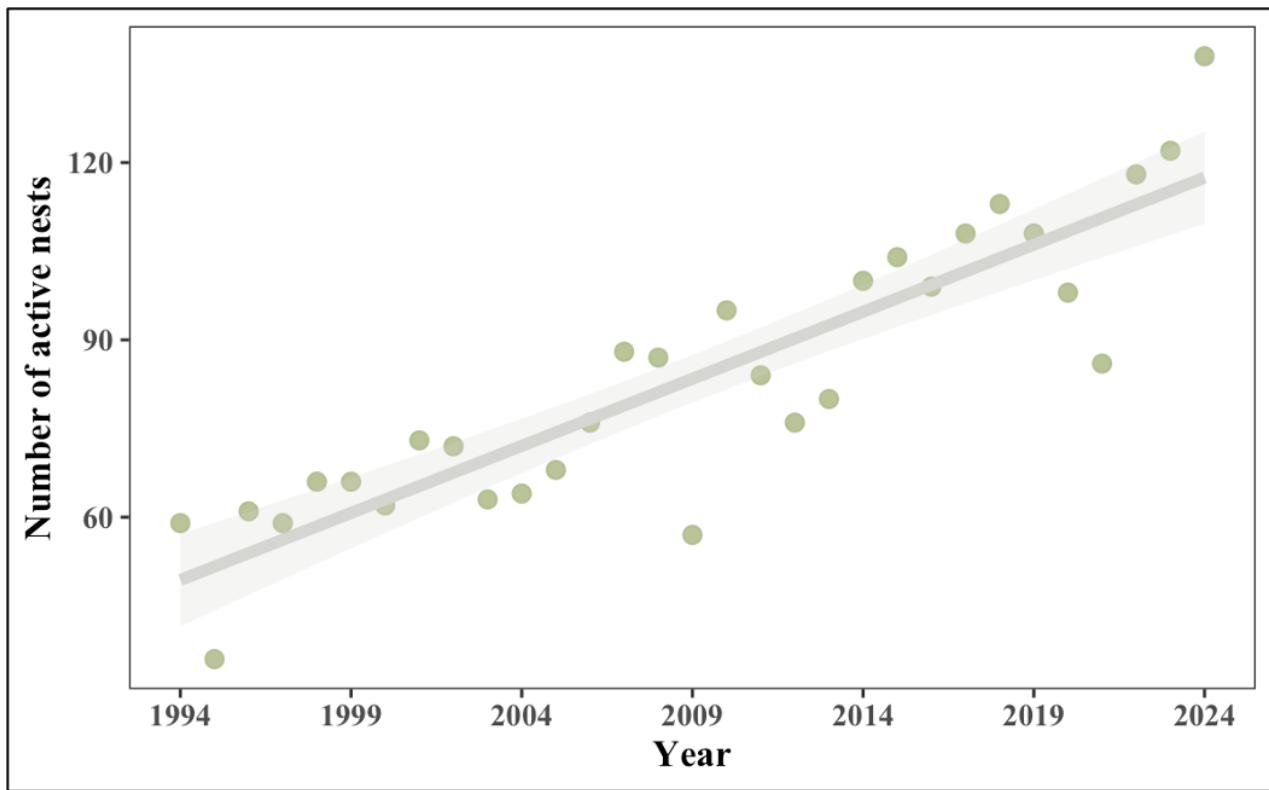


Figure 8: The number of active nests recorded for each breeding season across the study period.

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.

The strong temporal signal observed in Figure 1 was reflected in the model selection results (Table 1). 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 1: 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 ‘×’ 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)
Models including year trend							

Model	K	Deviance	AICc	Δ AICc	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	
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 2: 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 (corresponding to Fig. 1b–c). 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)
Models without year trend							
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	
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	

Model	K	Deviance	AICc	Δ AICc	w	R^2	slope (SE)
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 1 and Table 2, indicated that the number of active nests was weakly associated with weather variables. Models including a linear year trend in Table 1 corresponds with the causal structure represented by Figure 1a, where year is treated as a confounder and should be accounted for. Models excluding the year trend (Table 2) corresponds with the causal structures represented by Figure 1b and 1c. Under these scenarios, time was not treated as 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 (Δ 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 (Δ 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 (Δ AICc > 2). Models that included temperature predictors indicated moderate support, with all predictor variables ranging within Δ 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 showing poor received little support (Δ AICc > 7). Models excluding year (Table 2) addressed an alternative causal structure where the long-term temporal structures 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 (Δ 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.

4.2 Objective 2: Breeding success

Table 2. The model selection results relating annual weather variation to breeding success, quantified as the number of successful nests relative to unsuccessful nests, together with results from the analyses of including population size to the best supported model. Models were fitted using a binomial generalised linear mixed-effects model and year was added as a random effect. A ‘+’ between two predictor weather variables indicates additive effects, and ‘ \times ’ indicates an interaction term. The number of parameters is represented by K, with AICc being Akaike’s Information Criterion. ΔAICc represents the difference in AICc compared to the best supporting model, and w represents the Akaike weight. Deviance explained is comparable to R^2 . Regression coefficients (slope) with standard error are reported for the simple predictor models only.

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

Model	K	AICc	ΔAICc	w	Deviance explained	slope (SE)
Max temperature \times rainy days	5	234.93	8.01	0.008	0.104	
Population size comparison						
Minimum temperature			6.91	0.03	0.21	
Population size			5.44	0.06	0.24	
Minimum temperature + population size			0.00	0.91	0.50	

The model selection indicated that the breeding success had clearer associations with the weather variables included in the models (Table 2). The model showing the best support ($\Delta\text{AICc} = 0.00$, $w = 0.44$) is the single predictor model including minimum temperature, explaining the largest proportion of deviance compared to any of the other models (21%). The other models with single predictor variables explained little extra deviance and weak support relative to the best supported model ($\Delta\text{AICc} > 3$). The same was seen for models that had additive and interactive predictor variables, showing weak support compared to the best-supported model.

When accounting for population size in the best supported single predictor model, the combined model (minimum temperature + population size) was strongly supported ($\Delta\text{AICc} = 0$, $w = 0.91$) and accounts for 51% 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 and explains 21% of the annual variation in breeding success, in both scenarios.

Figure 9, showing the relationship between the predictor variable, minimum temperature and breeding success, indicates a positive relationship (slope = 0.167). Years with warmer temperatures have higher breeding success, as the upward trend suggests (Figure 2). The graphs also indicate that the observed breeding success varies substantially around the fitted relationship.

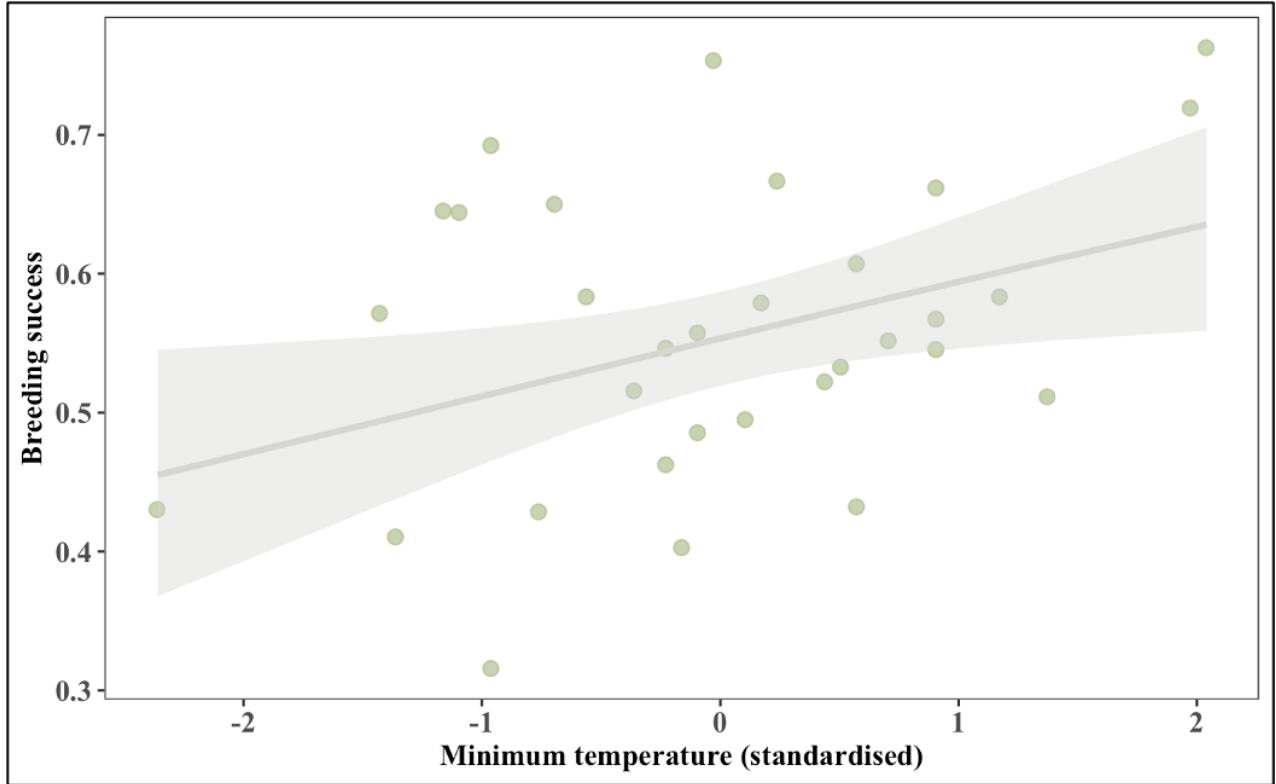


Figure 9: The relationship between minimum temperature and breeding success, expressed as the proportion of successful nests.

4.3 Objective 3: Breeding timing of successful nests

The breeding timing of successful nests was strongly associated with pre-laying weather conditions, with interactive effects between weather variables being the strongest predictors of the laying date (Table 3).

Table 3. Breeding timing of successful nests in relation to pre-laying weather conditions and population size. Model selection results relating breeding timing, quantified using estimated laying dates, to weather conditions during the 30-day pre-laying period at Dronfield. Models were fitted using linear regressions. A ‘+’ between predictor variables indicates additive effects and ‘×’ denotes an interaction. The number of parameters is represented by K , with AICc denoting Akaike’s Information Criterion; ΔAICc represents the difference relative to the best-supported model, and w indicates the Akaike weight. Adjusted R^2 represents the proportion of variance explained by each model. Regression coefficients (slope) with standard error are reported for simple predictor models only. Models including lagged weather predictors were fitted to a reduced dataset due to data availability and are therefore not directly comparable in AICc to models using current-year predictors.

Model	Deviance	<i>K</i>	AICc	Δ AICc	<i>w</i>	<i>R</i> ²	slope (SE)
Baseline							
Intercept only	482,345	2	12,615.63	1,279.63	0.000	0.000	
Temperature							
Minimum temperature (30 days)	230,069	3	11,529.94	193.94	0.000	0.499	-5.010 (0.131)
Mean temperature (30 days)	241,441	3	11,600.33	264.33	0.000	0.475	-5.478 (0.151)
Maximum temperature (30 days)	280,751	3	11,820.41	484.41	0.000	0.389	-4.775 (0.157)
Rain							
Rainy days (30 days)	404,580	3	12,360.96	1,024.96	0.000	0.161	-2.103 (0.126)
Total rainfall (30 days)	415,699	3	12,400.54	1,064.54	0.000	0.138	-0.286 (0.019)
Wind							
Maximum wind speed (30 days)	449,433	3	12,506.89	1,170.89	0.000	0.022	4.154 (0.727)
Mean wind speed (30 days)	452,345	3	12,516.32	1,180.31	0.000	0.016	4.397 (0.915)
Lagged effects							
Previous year's total rainfall	444,304	3	12,278.29	942.29	0.000	0.010	0.013 (0.003)
Previous year's rainy days	447,834	3	12,289.62	953.61	0.000	0.003	0.062 (0.032)
Previous year's mean temperature	448,801	3	12,292.70	956.70	0.000	0.000	-0.456 (0.576)
Joint effects							
Mean temperature + rainy days	203,047	4	11,349.65	13.65	0.001	0.558	
Mean temperature + mean wind speed	236,458	4	11,571.91	235.91	0.000	0.485	
Rainy days + mean wind speed	369,831	4	12,224.48	888.48	0.000	0.195	
Interactive effects							
Mean temperature \times rainy days	200,878	5	11,336.00	0.00	0.999	0.563	
Previous year's rainfall \times mean temperature	235,451	5	11,373.62	37.62	0.000	0.476	
Minimum temperature \times mean wind speed	215,500	5	11,438.51	102.51	0.000	0.531	
Population size comparison							
Mean temperature \times rainy days				65.56	0.00	0.56	

Model	Deviance	<i>K</i>	AICc	ΔAICc	<i>w</i>	R^2	slope (SE)
Population size				1,266.51	0.00	0.00	
Mean temperature \times rainy days + population size				0.00	1.00	0.58	

The breeding timing at Dronfield was best explained by an interaction effect of the mean temperature and the number of rainy days in the 30 day pre-laying period, with this interactive model receiving high support ($\Delta\text{AICc} = 0.00$, $w = 0.999$). Additionally, this best supported model accounted for 56.3% of the variation in laying date. The single predictor models showed poor support, showing high ΔAICc values regardless of the explanatory power of the models that included temperature, based on their R^2 values (Table 3). Similarly, single predictor models including rainfall also indicated weaker support relative to the best fit model. The previous year's weather conditions did not indicate a strong influence, and additive explained variance of the current breeding seasons, breeding timing ($\Delta\text{AICc} > 900$).

Laying dates of unsuccessful nests could not be estimated. A simulation examining the consequences of the unobserved laying dates of the unsuccessful nests indicated that if the effects are linear, the exclusion of the missing laying dates does not cause a systematic bias (See Appendix tbc).

The interactive model of mean temperature and rainy days received much less support when population size was not accounted for (Table 3). By combining the interactive model with population size, the model became the best supported model ($\Delta\text{AICc} = 0$, $w = 1$). Additionally, adding population size to the interactive model indicated a weak increase in explanatory power, increasing with approximate 0.02% from the interactive-only model.

5 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. 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).

Our finding is therefore best represented by the confounded causal structure (Figure 1a), 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.

Breeding success

Breeding timing of successful nests

6 Conclusion

7 Appendix

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