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

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Introduction

Climate change and weather variability

Climate change is widely projected to alter ecological systems by increasing the variability in weather patterns and the occurrence of extreme events across the globe. Events such as severe droughts, heat stress and flooding are predicted to become more frequent, leading to significant pressure on ecological systems. Many studies on the effects of climate change on environmental systems focus on shifts in mean climatic conditions, such as long-term change in precipitation, with less attention given to how increased variability may be driving ecological disruptions (Thornton *et al.* 2014). Although this emphasis has improved the understanding of mean climate trends, evidence suggests that inter-annual variation in climatic conditions plays a crucial role in the ecological response (Maxwell *et al.* 2018). Annual fluctuations in climatic conditions increase the unpredictability of environmental responses and often result in some years being more favourable than others, influencing the availability of important resources such as food, which can cause physiological stress to individuals, populations, and whole ecosystems. This results in substantial variation in the fitness and survival rates of species across multiple years, depending on the environmental conditions (Vázquez *et al.*2015, Berzins *et al.* 2020). Therefore, annual variability in climate is an often-overlooked driver of ecological response to environmental change, emphasising its importance in assessing the impacts of climate change on natural systems.

Effects of climatic variation on avian populations

Varying weather patterns, associated with climate change, include the increase in temperatures, fluctuation in rainfall regimes, and more frequent storm events. The way in which organisms and ecosystems respond to these climatic variables is an important component to help predict how climate change could affect biodiversity in the future (Cockrem 2022, Trew and Maclean 2021). In many animal species, the response to climatic variation often involves shifts in the timing of reproduction and migration, together with a change in foraging behaviour, dispersal and habitat selection (Cockrem 2022). TBC (add general ecological consequences of climate change, and end off with narrowing it down to birds)

Studying the consequences of changing weather patterns on avian population biology has become a major field of study over the years, with BirdLife International identifying extreme weather events

as the biggest threat to bird populations (Jenouvier 2013). Additionally, predicting the way in which bird populations respond to future climatic changes is of high demand to implement the most effective conservation strategies to mitigate any harmful consequences of climate change (Jenouvier 2013). It has been noted that weather conditions can alter metabolic rates, changes in adult bird body size, and influence the conditions during important activities, such as foraging and courtship, thereby affecting success (Crick 2004). Additionally, weather has an impact on the reproductive success and reproductive phenology of avian populations.

Weather conditions during the breeding period have direct consequences on chick survival through possible hyperthermic events or starvation due to conditions limiting foraging efficiency for the adult birds. Alongside the short-term effects of changing weather regimes on bird reproduction, the shift in environmental cues resulting from climate change influences the timing of when populations start to breed, and beyond the change in timing, the overall breeding performance is affected (Crick 2004, Møller *et al.* 2010). Despite variation across species, several studies have found that some species exhibit advanced breeding dates in response to weather conditions. Specifically, some species respond to warmer winters by laying eggs earlier than in colder years (Møller *et al.* 2010). Breeding performance is affected by documented changes in clutch sizes, egg size, and reproductive success, typically measured by whether a fledgling is produced, in response to the warming climate (Møller *et al.* 2010). TBC

Weather influences avian breeding success

The reproductive success of many organisms relies on numerous factors, including food availability, environmental conditions, population dynamics, and, importantly, their response to shifting climatic conditions. Consequently, this led to several studies focusing on how climate change is affecting important reproductive parameters, including reproductive success, timing of reproduction and clutch size, with significant effects found across multiple species (Nielsen and Møller 2006).

Conditions such as severe droughts, flooding, heat or cooling events reduce the survival rate and typically result in failed reproduction. In avian populations specifically, precipitation and temperature are known to affect the reproductive success of adult birds and the overall condition of the nestlings (Griebel and Dawson 2019). A study conducted by Dawson and Bortolotti (2000) on the reproductive

success of Kestrels found that in the event of inclement weather had significant effects on reproductive success, as nestlings were smaller in size and body mass, making a successful fledgling less probable compared to nestlings during more favourable conditions. The decreased probability of producing a fledgling could be due to either direct or indirect effects. The direct effects include extensive energy expenditure on thermoregulation during cooling events, causing significant chilling of the chicks, and indirect effects include reduced hunting effort and prey delivery to the nest by parent birds (Dawson and Bortolotti 2000). Additionally, significant impacts of inclement weather are seen over periods as short as 3 days, leading to either partial or complete brood failure and decreased fledging success (Dawson and Bortolotti 2000).

Vultures

Across the globe, there are 23 vulture species, most of them within the family Accipitridae and the remaining species within the family Cathartidae, 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 (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). These life-history traits make vultures especially vulnerable to reduced reproductive success, which has long-term consequences for future population stability.

African White-Backed Vultures

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.* 2017). 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.* 2017).

To be added somewhere Reductions in breeding success, reproductive investments, or missed breeding seasons, driven by weather fluctuations, often lead to population declines, especially in long-lived species where recruitment depends on the repetition of successful breeding seasons (Andreasson *et al.* 2020) 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.

Warmer years are noted to have earlier egg laying dates as most bird species aim to correspond laying dates with periods of high food availability (Andreasson *et al.* 2020).

Aims and Objectives

By analysing 31 years of breeding data alongside local weather data, this project aims to determine if, and how, weather affects the reproductive timing and success of African White Backed Vultures. To address this, three main objectives were identified:

1. To assess whether annual weather variation is associated with varying number of active nests of African white-backed vultures, measured in the total number of nests per year.

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 and wind, prolonged rainfall and increased storm events.

2. To assess whether annual weather variation is associated with varying annual breeding success in 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 and 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 the breeding timing of white-backed vultures.

We hypothesise that the breeding timing, measured in laying dates, is influenced by the weather conditions in the 60 days prior to laying periods, which reflects white-backed vulture sensitivity to environmental cues before breeding.

Methods

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.

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 standarised 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.

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).

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.

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

DAGS (TBC)

Number of Active Nests
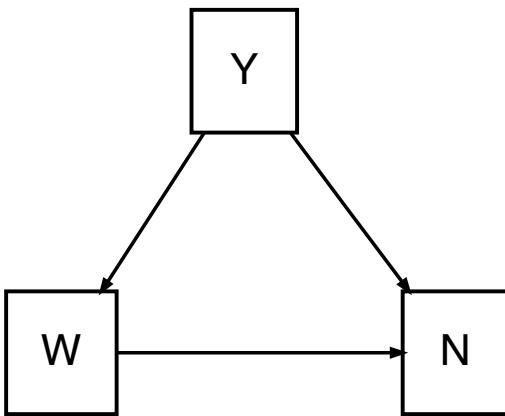
Figure 1: Number of Active Nests Scenario A

In this scenario, the temporal trend (Y) directly influences both weather (W) and breeding effort (B). Because Y affects both variables, it acts as a confounder of the weather–breeding relationship. To

estimate the direct effect of weather on breeding effort, it is therefore necessary to control for Y in the analysis.
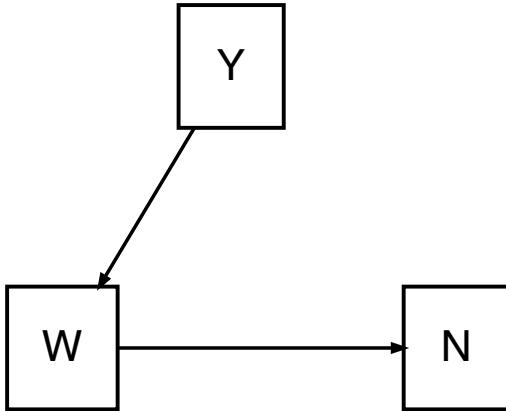

Figure 2: Number of Active Nests – Scenario B

In this scenario, the temporal trend (Y) influences the weather variable (W), which in turn affects breeding (B). There is no direct effect of the trend on breeding, meaning that Y is not a confounder of the weather–breeding relationship. As a result, controlling for Y is unnecessary and could obscure the effect of interest, since the influence of Y on breeding operates entirely through weather.
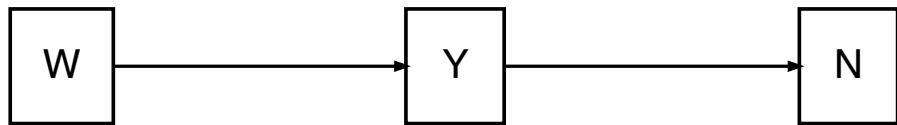
Figure 3: Number of Active Nests Scenario C

In this scenario, the temporal trend (Y) acts as a mediator of the weather effect on breeding effort, with weather influencing Y and Y in turn affecting breeding. Because Y lies on the causal pathway between weather and breeding, controlling for Y would block part of the effect of interest. To estimate the total effect of weather on breeding effort, Y should therefore not be included as a control variable.

Breeding timimg of succesfull nests
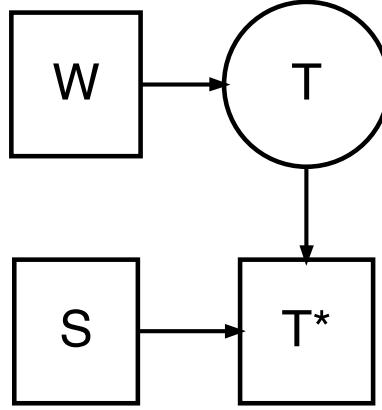
Figure 4: Timimg scenario A.

In this scenario, weather (W) does not affect breeding success (S), meaning that success is effectively random with respect to the weather variable used to explain breeding timing. As a result, success does not act as a confounder, and analysing observed timing (T*) yields the correct inference about the effect of weather on timing. This situation is plausible if breeding success is driven mainly by conditions later in the breeding season, rather than by the pre-breeding weather cues that influence the initiation of breeding.
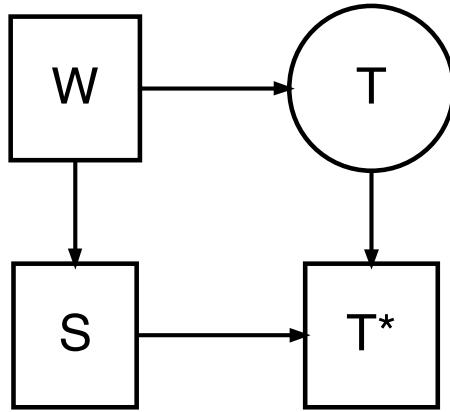
Figure 5: Timimg scenario B.

In scenario (b), the same weather variable (W) influences both breeding timing (T) and breeding success (S), but timing itself does not causally affect success. In this case, success is associated with weather, and observed timing (T^) is therefore indirectly linked to weather through both pathways. However, because success is not a mediator of the weather–timing relationship, analysing T* can still recover the underlying effect of weather on timing, particularly when effects are approximately linear. The simulation results suggest that under this structure, any bias introduced by observing timing only

for successful nests is small and unlikely to alter biological interpretation.
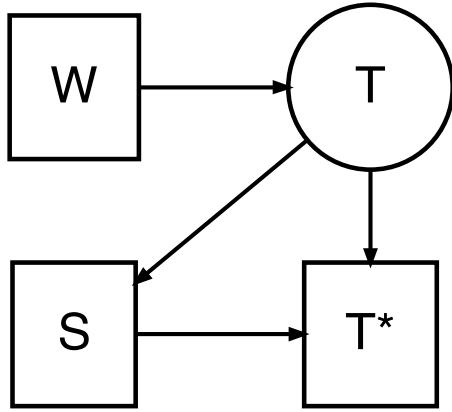
Figure 6: Timing scenario C.

In scenario (c), breeding timing directly influences breeding success, in addition to weather affecting timing. Under this structure, it is no longer possible to disentangle whether an apparent effect of weather on observed timing reflects a direct causal effect on breeding initiation or an indirect effect mediated through success. In this case, inference is limited to the timing of successful nests only. Although this scenario may seem plausible at first, it is less clear at the interannual scale considered here, as selection on early or late breeding within a season does not necessarily imply that years with earlier or later average breeding are associated with higher or lower overall breeding success.
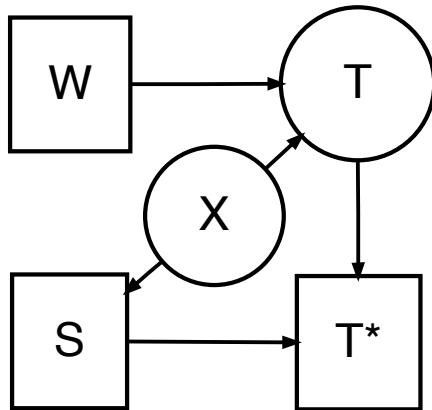
Figure 7: Timimg scenario D.

In scenario (d), an unobserved variable (X), representing colony state or population size, influences both breeding timing (T) and breeding success (S). In this case, population-level processes such as density dependence, food competition, or overall adult condition could shift both when breeding is initiated and the likelihood of breeding success. Because X affects both timing and success, it acts as

a confounder, and the effect of weather on observed timing (T*) cannot be cleanly isolated without accounting for this shared influence. If a suitable proxy for colony size or population state were available, including it in the analysis could help reduce this source of bias; otherwise, inference about causal pathways remains uncertain.

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.

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).
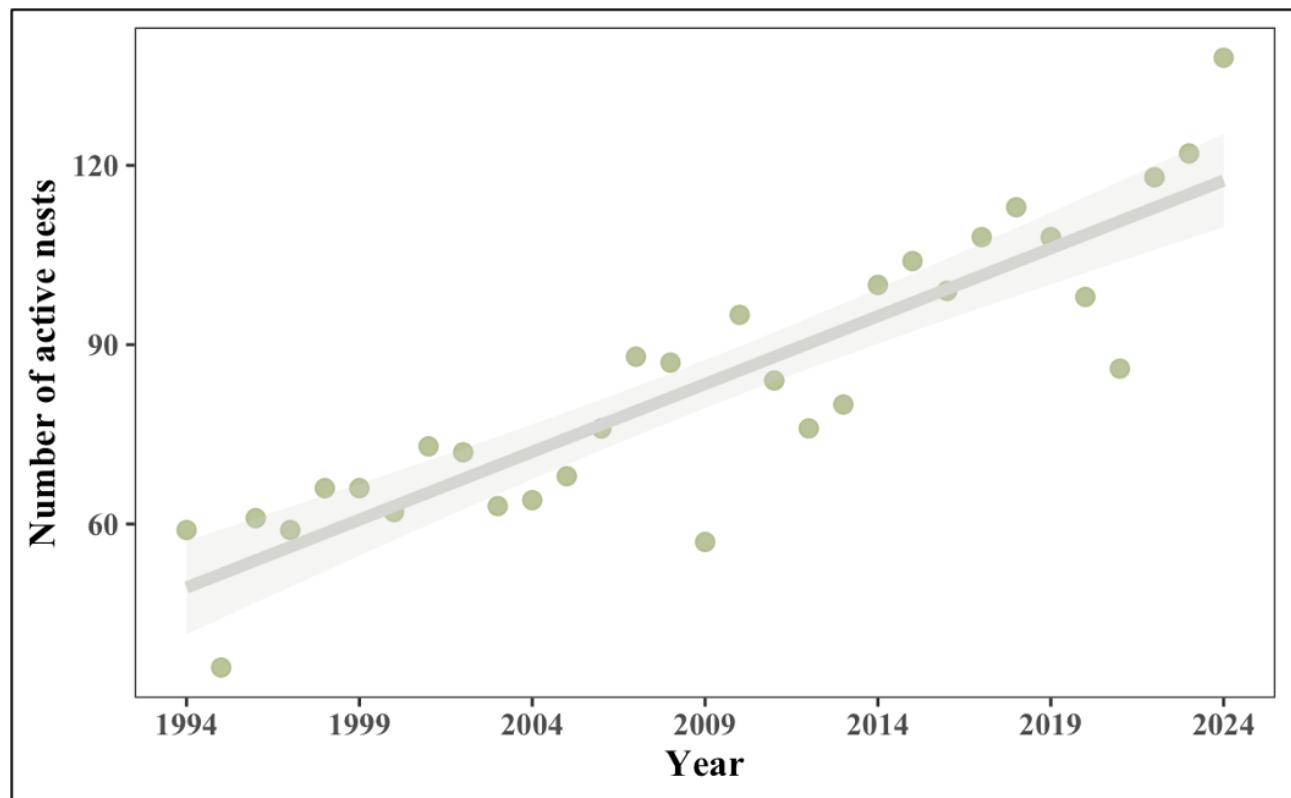

Figure 8: The number of active nests recorded for each breeding season across the study period.

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. Model selection results relating to annual weather variation and the number of active nests at Dronfield (1993–2024). Models were fitted using linear regressions. Results for models with and without a linear year effect are shown to reflect causal assumptions regarding temporal trends. A '+' indicates additive effects and '×' indicates an interaction. K is the number of parameters; AICc is Akaike's Information Criterion; ΔAICc is relative to the best model; w is the Akaike weight; adjusted R^2 is variance explained. Slopes (SE) are reported for simple predictor models only.

Model	K	Deviance	AICc	ΔAICc	w	Adj. R^2	slope (SE)
Models including year trend							
Baseline							
Year (baseline)	3	0.6	-28.43	0.64	0.14	0.759	
Rain							
Maximum daily rainfall	4	0.5	-29.07	0	0.193	0.775	-0.002 (0.001)
Total rainfall	4	0.5	-27.49	1.58	0.088	0.764	0 (0)
Previous year's total rainfall	4	0.6	-25.81	3.27	0.038	0.751	0 (0)
Rainy days	4	0.6	-25.78	3.29	0.037	0.75	0 (0.002)
Temperature							
Minimum temperature	4	0.6	-26.68	2.39	0.058	0.757	0.016 (0.017)
Mean temperature	4	0.6	-26.59	2.48	0.056	0.757	0.026 (0.03)
Maximum temperature	4	0.6	-26.42	2.65	0.051	0.755	0.01 (0.013)
Wind							
Maximum wind speed	4	0.6	-25.9	3.18	0.039	0.751	-0.002 (0.006)

Model	K	Deviance	AICc	ΔAICc	w	Adj. R^2	slope (SE)
Mean wind speed	4	0.6	-25.87	3.21	0.039	0.751	-0.019 (0.07)
Hail							
Hail days	4	0.6	-25.88	3.19	0.039	0.751	0.006 (0.02)
Joint effects							
Min temperature + max daily rainfall	5	0.5	-27.44	1.63	0.085	0.776	
Max daily rainfall + max wind speed	5	0.5	-26.41	2.66	0.051	0.769	
Min temperature + total rainfall	5	0.5	-25.04	4.03	0.026	0.758	
Min temperature + max wind speed	5	0.6	-23.83	5.24	0.014	0.749	
Max temperature + rainy days	5	0.6	-23.78	5.29	0.014	0.748	
Hail days + max wind speed	5	0.6	-23.12	5.95	0.01	0.743	
Hail days + rainy days	5	0.6	-23.03	6.04	0.009	0.742	
Interactions							
Prev. rainfall × max temperature	6	0.6	-21.36	7.71	0.004	0.744	
Min temperature × mean wind speed	6	0.6	-21.3	7.77	0.004	0.744	
Min temperature × rainy days	6	0.6	-21.04	8.03	0.003	0.741	
Models without year trend							
Baseline							
Intercept only	2	2.5	14.26	2.22	0.057	0	
Rain							
Total rainfall	3	2.2	12.83	0.79	0.117	0.088	-0.001 (0)
Previous year's total rainfall	3	2.4	15.07	3.03	0.038	0.019	0 (0)
Maximum daily rainfall	3	2.4	15.74	3.7	0.027	-0.002	-0.003 (0.003)
Rainy days	3	2.5	16.72	4.68	0.017	-0.034	0 (0.003)
Temperature							
Maximum temperature	3	2.2	12.77	0.74	0.12	0.089	0.046 (0.023)
Mean temperature	3	2.5	16.46	4.42	0.019	-0.026	0.031 (0.062)
Minimum temperature	3	2.5	16.61	4.58	0.018	-0.031	0.011 (0.036)

Model	K	Deviance	AICc	ΔAICc	w	Adj. R^2	slope (SE)
Wind							
Maximum wind speed	3	2.3	14.39	2.35	0.054	0.041	-0.016 (0.011)
Mean wind speed	3	2.3	14.84	2.81	0.043	0.026	-0.18 (0.134)
Hail							
Hail days	3	2.1	12.04	0	0.174	0.111	0.076 (0.035)
Joint effects							
Hail days + max wind speed	4	2	13.16	1.12	0.099	0.123	
Max temperature + rainy days	4	2.1	14.37	2.33	0.054	0.088	
Hail days + rainy days	4	2.1	14.44	2.4	0.052	0.086	
Min temperature + total rainfall	4	2.2	15.45	3.41	0.032	0.056	
Max daily rainfall + max wind speed	4	2.2	15.84	3.81	0.026	0.044	
Min temperature + max wind speed	4	2.3	17.03	5	0.014	0.006	
Min temperature + max daily rainfall	4	2.4	18.24	6.2	0.008	-0.033	
Interactions							
Prev. rainfall × max temperature	5	2	15.71	3.67	0.028	0.1	
Min temperature × mean wind speed	5	2.3	20.27	8.23	0.003	-0.043	
Min temperature × rainy days	5	2.5	21.95	9.92	0.001	-0.101	

Model selection represented by Table 1, indicated that the number of active nests was weakly associated with weather variables. The single predictor model including maximum daily rainfall was best supported among models including the year effect (ΔAICc = 0.00, w = 0.19) despite its small effect size (slope = -0.002). 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 (ΔAICc =0.64, w = 0.14). The number of rain days and the lagged rainfall (based on the previous year's rainfall) showed limited support (ΔAICc > 2). Models that included temperature predictors indicated moderate support, with all predictor variables ranging within ΔAICc = 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 (ΔAICc > 7). Candidate models that excluded the effect of year indicated weak support. Additionally, increasing model complexity did not improve the model support, with single predictor models performing better than the poorly supported interactive, and additive models (ΔAICc > 7).

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 '×' 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						

Model	K	AICc	ΔAICc	w	Deviance explained	slope (SE)
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 × wind speed	5	232.04	5.11	0.034	0.225	
Max temperature × 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 (ΔAICc = 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 (ΔAICc > 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 (ΔAICc = 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.
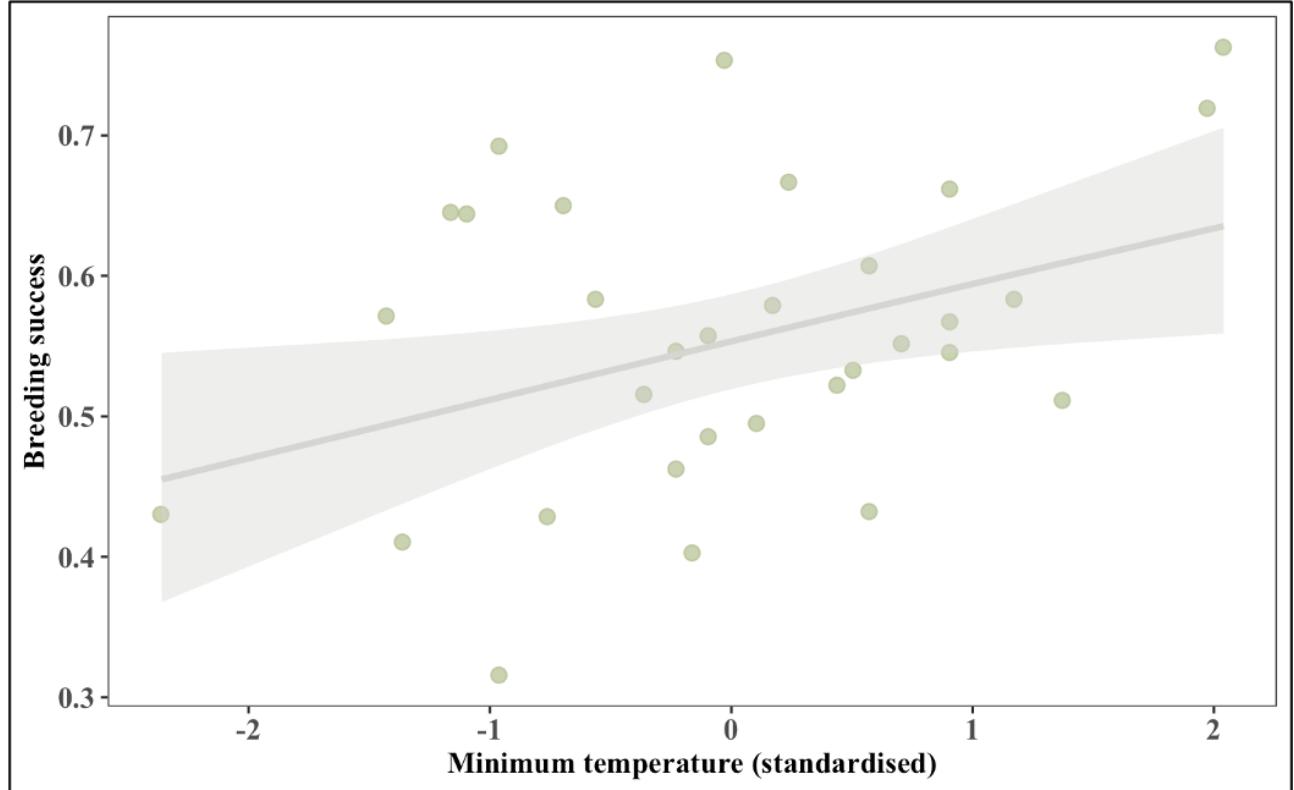

Figure 9: The relationship between minimum temperature and breeding success, expressed as the proportion of successful nests.

Objective 3: Breeding timing of succesful 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	K	AICc	ΔAICc	w	R^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	

Model	Deviance	K	AICc	ΔAICc	w	R^2	slope (SE)
Previous year's rainfall × mean temperature	235,451	5	11,373.62	37.62	0.000	0.476	
Minimum temperature × mean wind speed	215,500	5	11,438.51	102.51	0.000	0.531	
Population size comparison							
Mean temperature × rainy days				65.56	0.00	0.56	
Population size				1,266.51	0.00	0.00	
Mean temperature × 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 (ΔAICc = 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 R2 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 (ΔAICc > 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 (ΔAICc = 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.