Return of the white stork: a study of the population viability and habitat preferences of a novel population

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Contents

Abstract

Reintroductions are often utilized in rewilding projects to aid in the restoration of self-sustaining ecosystems. However, reintroductions are challenging so to increase the probability of a reintroduction's success it is recommended that extensive knowledge should be gained on the target species to support adaptive management strategies and identify risks to that population's establishment.

This thesis will focus on the recent reintroduction of the European white stork (*Ciconia ciconia*) to the UK. Firstly, to explore the impact that different management strategies and migratory behaviour has on this population's long-term viability, a population viability analysis (PVA) was conducted. The PVA demonstrated that if a small proportion of the British population overwinters in the UK the population would achieve a positive growth rate without additional management actions due to this behaviour's associated lower mortality rates. Alternatively, management actions that increased fledglings per nest produced a 54.3% increase in population size after 50 years whilst combining all the explored management options produced a 378.3% increase.

Secondly, field data was collected to develop habitat suitability models to understand which habitat variables are associated with the population's foraging behaviour during the breeding season. White storks were shown to prefer foraging in open areas close to their nests and water. White stork presence was also positively correlated to an open-air pen where injured storks were fed. Grass height was only identified as a significant explanatory variable at the micro-scale, with white storks preferring areas with shorter grass. Disturbance by walkers and the number of livestock were not influential at their current levels.

This thesis suggests a positive future for the white storks in the UK but recommends continuous close monitoring of this novel population. As more data becomes available these models can be updated to support this reintroduction more effectively and increase the probability of its success.

1. Introduction

1.1 Rewilding and Reintroductions

Rewilding was first formally described by Soulé and Noss in 1998 as a strategy that focused on protecting and restoring native biodiversity through the establishment of core wildness areas connected with corridoes and returning keystone species to their native range (Soulé & Noss, 1998). Since this publication it has become increasingly popular across the world, yet rewilding's popularity has also led to one of its great weaknesses, with the concept regularly evolving to encapsulate a broad range of themes and theories leading to wide array of occasionally conflicting definitions (Johns, 2019; Jørgensen, 2015; Prior & Ward, 2016). The term rewilding has been used to refer to the reintroduction of megafauna to recreate landscapes from the Pleistocene (Donlan et al., 2006), to passive land abandonment of unprofitable agricultural landscapes (Carver, 2019) to restoring top-down trophic interactions and associated trophic cascades (Svenning et al., 2016) and much more (Johns, 2019). This ambiguity is often a source criticism and can lead to difficulty with its implementation as well as measuring the concepts potential ecological or socio-economic benefits (Hayward et al., 2019; Pettorelli et al., 2018). To provide some clarity, the IUCN's Commission on Ecosystem Management (CEM) Rewilding Thematic Group (RTG), consulted with over 150 rewilding experts, to consolidate the literature and support the incorporation of rewilding into global conservation targets (Carver et al., 2021; IUCN, 2021**)**. Following the consultation, they presented ten guiding principles and defined rewilding as "the process of rebuilding, following major human disturbance, a natural ecosystem by restoring natural processes and the complete or near complete food web at all trophic levels as a self-sustaining and resilient ecosystem with biota that would have been present had the disturbance not occurred" (Carver et al., 2021). Whilst this did provide some clarity to the concept, it did not fully succeed in ending the debates and there is still much conversation around how the principles should best be interpreted or implemented (Schulte to Bühne et al., 2022). However, the emphasis on creating self-sustaining ecosystem services with minimal ongoing management has continued and is a common goal in rewilding projects today (Pettorelli et al., 2018; Rewilding Europe, 2021; Sweeney et al., 2019; Wrigley & Driver, 2022).

The process of restoring ecosystems and their associated biodiversity requires an understanding of what led to the initial degradation (IUCN, 2013). The cascading negative impacts of species extinction has been well documented, including the destabilisation of wider ecological communities, the loss of ecosystem services and reducing the resilience of that ecosystem to future disturbances (Cardinale et al., 2012; Oliver et al., 2015; Seddon et al., 2014). Therefore reintroductions, here defined as the intentional movement and release of a species to re-establish a viable population within its native range (IUCN, 2013), can aid in the restoration of these functions and services to create selfregulating, biodiverse ecosystems (Corlett, 2016; Svenning et al., 2016). Consequently, reintroductions are often a component of rewilding projects, generally focusing on species whose presence can greatly influence ecosystem processes (Seddon & Armstrong, 2019; Svenning et al., 2016). This could be through the reintroduction of apex predators such a wolves that can reinitiate trophic cascades leading to changes in prey behaviour and vegetation dynamics (Ripple & Beschta, 2012) or the reintroduction of ecosystem engineers such as beavers or large herbivores which can create substantial changes to the environment through behaviours such as dam building or grazing that can have significant consequences to the wider ecological community (Haynes, 2012; Naundrup & Svenning, 2015; Stringer & Gaywood, 2016).

However, reintroducing a species is not a simple task and can be prone to failure (Berger-Tal et al., 2020). Sometimes these failures arise from anthropogenic sources, such as a lack of administrative support, reduction in funding or resistance from local residents (Berger-Tal et al., 2020; Watkins et al., 2021). In other cases, there have been insufficient knowledge of the species habitat requirements prior to release leading to poor-quality release sites or unexpected interactions with other species within the area (Bennett et al., 2013; Bubac et al., 2019; Hardman et al., 2016). The small populations often used in reintroductions are also inherently vulnerable to genetic risks such as founder's effects or inbreeding which the impacts of may not be visible until a few generations have passed (Jamieson, 2011). Considering these concerns, it is recommended that practitioners seek extensive knowledge the released species ecology and behaviour and closely monitor the population's progress, adjusting management strategies as needed to maximise the probability of a reintroduction's success (Berger-Tal et al., 2020; IUCN, 2013).

1.2 Subject Species: The White Stork (*Ciconia ciconia*)

The European white stork (*Ciconia ciconia*) is a long-distance migratory bird which can be found across Europe typically arriving in March and leaving in August (Hancock et al., 1992). They are commonly associated with non-intensive agricultural landscapes, wetlands, and human settlements, with breeding pairs typically returning to the same nest each year (Nowakowski, 2003; Vergara et al., 2010).

They are occasionally classed into two subpopulations based on their diverging migration behaviour, with individuals either migrating through western Europe across the Straits of Gibraltar towards the Sahel region or through eastern Europe via Turkey and wintering in eastern and southern Africa (Kanyamibwa et al., 1993). The route taken is largely dependent on geographical location with the dividing line in central German but mixing naturally occurs between the two subpopulations (Shephard et al., 2013).

White storks are opportunistic foragers, able to consume a wide variety of invertebrates, rodents, fish, reptiles and amphibians, the quantities of each largely dependent on what is in the local habitat (Antczak et al., 2002; Chenchouni, 2017). They can also effectively utilize anthropogenic food sources such food waste in landfills and invasive crayfish found in rice fields which has contributed to the emergence of large non-migratory populations particularly in the Iberian Peninsula (Ferreira et al., 2019; Gilbert et al., 2016).

Currently the species is categorised at 'Least Concern' by the IUCN with the European population is estimated to be around 224,000-247,000 pairs (BirdLife, 2022). However, the species experienced significant population declines during the 20th century, with local population extinctions occurring in many western European countries (Luthin, 1987; Thomsen & Hötker, 2013). This population decline has been largely attributed to significant changes in land use such as draining wetlands, changes in crop rotations and the increased pesticide use as agricultural practices intensified, resulting in loss of high-quality breeding habitat and their associated food items (Donald et al., 2001; Luthin, 1987; Verhoeven, 2014). These population declines were further exacerbated by long periods of dry weather in the Sahel wintering grounds and collisions with powerlines (Demerdzhiev, 2014; Kaługa et al., 2011; Kanyamibwa et al., 1993).

In response to these declines, several reintroduction and population recovery programmes were formed to restore the western white stork populations. The first programme was initiated in Switzerland in 1948 when the Swiss population was on the verge of extinction (Moritzi et al., 2001). A small group of juveniles were imported from other European populations and were further supplemented by individuals from north-west Africa. These birds were hand reared and then released when they reached fledgling age, but few returned to their rearing place the following year. In response, fledglings were kept for longer in captivity until they reached sexual maturity at three years of age which enhanced their survival expectations but also resulted in the white storks losing their desire to migrate once released, becoming reliant on supplementary feeding to survive the winter (Hancock et al., 1992; Moritzi et al., 2001; Schaub et al., 2004). Regardless these storks were successfully, and over the following decades the number of free-flying individuals steadily increased and began migrating along the Western Flyway and returning, attracted to the permanent non-migratory population in Switzerland (Jenni et al., 1991). Over the time the amount of supplementary feeding decreased with 669 breeding pair counted in 2020, and number that is anticipated to increase (Keystone-SDA, 2020; Schaub et al., 2004).

Other reintroduction and reinforcement projects followed in Belgium, Netherlands, France, Sweden and Spain in 1957, 1969, 1976, 1989 and 2003 respectively, often utilising a mixture of management methods, including supplementary feeding, providing nesting platforms, maintaining a stationary population to encourage birds to return, releasing selection of the birds only upon sexual maturity and supplementing the population with captive-bred juveniles to encourage migratory behaviour (Doligez et al., 2004; Galarza & García, 2012; Gow et al., 2016; Olsson, 2007; Thomsen & Hötker, 2013; Wei-Haas, 2015).

The history the white stork within the UK is less clear than mainland Europe with the last known breeding of wild white storks in Edinburgh in 1416 on St Giles Cathedral, which was recorded by the chronicler Walter Bower (Gurney, 1921). Looking further back, there is archaeological evidence to suggest the species was present in southern England during the Roman period, with white stork bones being unearthed with roman remains near Silchester, Hampshire (Parker, 1988; Serjeantson, 2010). Following this, the village of 'Estorchestone', a name which means 'homestead for storks', and now present day Storrington, was recorded with the Domesday Book in 1086 (Powell-Smith, 2022). Moving into the medieval period, illustrations of white storks were featured in bestiaries and were also recorded being sold at the London game markets as late as 1507 (Fair, 2016; Macdonald, 2019). Whilst this does not guarantee the species was commonly breeding in the UK, without the means of preservation and fast travel, such a market would be improbable unless the birds were harvested from the local landscape. So, whilst it is unlikely that the British white stork population was substantial in size, such recordings suggest that white stork did historically reside and breed in Great Britain at the edge of its natural range. Their subsequent extinction has been attributed to a mixture of overhunting, persecution and loss of wetland habitats (Macdonald, 2019). Since then, white storks have regularly managed to cross the English Channel from the European mainland with over 1115 sightings of white stork being recorded between 1958 and 2013 (Gow et al., 2016; White & Kehoe, 2016). A few breeding attempts of escaped captive bred storks in the UK have also occurred although none were successful (BBC, 2014; Cocker & Mabey, 2005). However, even with these sightings and breeding attempts, the chance of a successful white stork recolonisation without human intervention is low due to the species gregarious nature as colonial nesters, often attracted to larger colonies and typically dispersing along pre-existing migration routes (Ječmenica & Kralj, 2017).

1.3 Reintroducing the White Stork to the UK

The white stork reintroduction formally began in 2016 with 3 reintroductions sites in southern England; the Knepp Castle Estate in West Sussex, Wadhurst Park in East Sussex, and Wintershall Estate on Surrey. These sites are working collaboration with the Cotswold Wildlife Park and Gardens, Roy Dennis Wildlife Foundation, Warsaw Zoo and the Durrell Wildlife Conservation Trust to form the White Stork Project (WSP). Their main goal is to produce a self-sustaining population of 50 breeding pairs of white storks in Sussex area by 2030 as well as provide socio-economic benefits to the local communities.

The reintroduction builds upon the knowledge gained from the previous European reintroductions and consists of three main elements. In response to the initial difficulties of the Swiss reintroduction, the project first established sedentary populations of white storks to act as an 'anchors' to encourage flying white storks to return after migrating. An open-air, predator proofed pen can be found at all three reintroduction sites each contain roughly 30 birds provided by Warsaw Zoo that can no longer fly due to sustaining previous injuries. Secondly, 46 flying adults were retained in the pen at the Knepp Castle Estate and slowly released over the course of three years to increase the likelihood of them remaining and breeding at the reintroduction site. Consequently, few of these birds exhibit traditional migratory behaviour. Lastly, Cotswold Wildlife Park provide 20-40 captive-bred juveniles from their white stork breeding programme which are released from the Knepp reintroduction site from 2019 to 2023 in late summer to reinforce the population and encourage a migratory behaviour.

When consider the rewilding lens this reintroduction is being conducted through the addition of the white stork into southern England is unlikely to result in the dramatic ecosystem changes that large herbivores or predator can initiate, however they could function as gentler ecosystem engineers. Their large nests can provide nesting habitats for small birds such as house sparrows and starlings, providing valuable protection from predators eventually causing tree mortality (Bocheński, 2005; Zbyryt et al., 2017). Additionally the transportation of nesting material can also assist with seed dispersal, with other 9000 seedlings from 97 taxa being collected from Polish stork nests(Czarnecka & Kitowski, 2013). The WSP also places a heavy emphasis of public engagement at the reintroduction sites and through giving talks about the project and having an active social media presence to educate the public on the reintroduction and rally support. In several European countries the white stork has been recognised as a flagship species for wetland and grassland conservation in part due to the species' popularity and cultural significance as it is often associated with good luck and happiness when they return to their nests each spring (Buitenhuis & Prummel, 2001). Therefore, the return of this charismatic bird may have the potential to reengage the British public with the natural world and support the restoration efforts of their associated habitats (Kronenberg et al., 2017; Olsson and Rogers, 2009; Thomsen and Hötker, 2013).

As the Knepp Castle Estate is the primary reintroduction site where the majority of management actions are taking place this thesis will focus on the population that resides there. The Knepp Castle Estate is a 3,500-acre estate located near Horsham which once predominantly consisted of a mixture of arable and dairy farming. However, the heavy Low Weald clay which the farm rests upon was incompatible with the heavy machinery required for modern intensive farming and so farming the land became increasingly financially unviable. It was in 2001 when the estate began restoring the farmland and were largely inspired by Franz Vera's (2000) theory of cyclical vegetation turnover which argued that historically, lowland Europe was not closed forest landscape, but a shifting, park-like mosaic where tree regeneration was suppressed by large herbivores. Over the following years free ranging long-horn cattle, Exmoor ponies and Tamworth pigs were added to the estate alongside the pre-existing red, fallow and roe deer populations with the intention that their different grazing, browsing and foraging techniques would lead to the creation of a diverse, heterogenous landscape. Due to the absence of predators, the estate harvests 75 tonnes of meat to manage the livestock population size and provide an additional source of income (Knepp Wildland, 2022a). Today Knepp is as rewilding flagship for the UK and boasts a wide range of biodiversity including breeding populations of nightingales, turtledoves and the largest population of purple emperor butterflies in the country which has increased ecotourism to the estate (Knepp Wildland, 2022b).

1.4 Thesis Aims

Even though they have been several white stork reintroduction projects across Europe and subsequent literature discussing and evaluating their varying strategies and outcomes there is very little data on the British population at this early stage of the reintroduction. Hence the overall aim of this thesis is to gather information to understand what essential demographic and environmental parameters need to be met to increase the reintroduction's likelihood of success as there is limited literature on the historical presence and subsequent decline of white storks in the UK and how they utilized the landscape.

In the first chapter a population viability analysis (PVA) was conducted using the software *Vortex 10.5.20* (Lacy, 2019) to identify what parameters, need to be met to achieve a self-sustaining white stork population within the UK. *Vortex10* is an individual-based simulation model where a population is subjected to a combination of deterministic environmental, demographic and genetic stochastic events based on defined probabilities (Brook et al., 1999). The models were constructed using a mixture of data on the British population that was further supplemented be studies on other European stork populations. With this tool the long-term viability of this reintroduced population was assessed and impacts of different management scenarios and migratory behaviour on the population's growth rate were compared.

In the second chapter, field data was collected on the white stork population at the Knepp Castle Estate during the chick-rearing period in the summer of 2022 with the aim to identify which habitat variables significantly influence their foraging preferences. During the breeding season the white stork's foraging range is significantly limited to a 5km radius around their nest, so the availability of high-quality is essential for reproductive success (Johst et al., 2001). Habitat suitability models provide a way to spatially understand a species' niche requirements as well as predicting other locations that may be suitable or need improving (Guisan & Zimmermann, 2000). The variables measured during the survey period included the impacts of human disturbance, vegetation structure, distance to key features and the presence of herbivores. This data was then used to develop habitat suitability models at both local and micro scales to and a habitat suitability map was created to identify the availability of suitable habitat at the reintroduction site. By studying this reintroduction project in its infancy, potential threats can be identified early providing more time for any management solutions to be explored, thus improving the chances of reintroduction success.

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2. Chapter 1: Demographic consequences of management actions for the successful reintroduction of white storks (*Ciconia ciconia*) in the UK[1]

2.1 Abstract

Species reintroductions are increasingly being used in conservation management practices to increase biodiversity and aid in the restoration of ecosystem function. For reintroductions to be successful, it is important to identify the conditions required for the establishment of viable populations. We developed a demographic model using *Vortex10* to assess the long-term consequences of different management interventions on the success of the reintroduction of white storks (*Ciconia ciconia*) in the UK. Demographic data obtained from the recently reintroduced population to southern England was supplemented with parameter information from western European populations to build the models. The impact of incorporating different management actions (e.g., supplementing with captive-bred juveniles, provision of nest platforms and habitat improvement/ supplementary feeding) on the stochastic population growth rate was assessed. Survival rates also differ depending on the migratory strategy individuals adopt, hence we tested the impact of having different proportions of the population as resident or migratory.

Our models show that if the British stork population adopts a fully migratory strategy with its associated higher mortality rates i.e., all individuals migrating to southern Europe or northern Africa, increasing the supplementation rate of juvenile birds alone would not lead to a positive population growth rate. However, including management actions to increase in the number of fledglings per nest produced a 54.3% increase in population size after 50 years and, when combining all three management options, the population grew by 378.3%. Alternatively, if a minimum of 9% of individuals established as non-migratory in Britain, which is likely to be the case based on field observations and tracking data, additional management actions would not be needed to achieve a positive growth rate due to associated lower mortality rates.

We conclude that the British white stork population will likely be viable in the long-term with the current management practices, but these models and projections should be updated as more demographic and stochastic data on this novel population becomes available.

[1] This chapter is an earlier draft of the paper with the same title by Mayall *et al.* (2023) hence the content varies between this version and the one that was published.

2.2 Introduction

Despite international commitments, global biodiversity loss has accelerated in the past 50 years (Diaz *et al.*, 2019; Pereira *et al.*, 2020) Within Europe, changes in land use and overexploitation are considered to be among the main causes for defaunation, with many species experiencing range reductions, decreases in population size or local extinctions (Diaz *et al.*, 2019; Henle *et al.*, 2008). Such losses can have cascading negative effects, reducing the resilience of ecosystem functions and the stability of ecological communities (Cardinale *et al.*, 2012; Oliver *et al.*, 2015). Reintroductions, the intentional movement and release of a species to re-establish a viable population within its native range, is one conservation measure that has been increasingly explored as a solution to Europe's dramatic biodiversity decline. (IUCN, 2013; Pereira *et al.*, 2020; Seddon *et al.*, 2014).

Reintroductions are often incorporated into rewilding projects as the act of returning a species to its native range not only has the potential to benefit the focal species, but can also aid in the restoration of ecosystem function and services which are important elements of rewilding (Naundrup & Svenning, 2015). Although the definitions of rewilding are fluid, leading to difficulty in measuring the success of its implementation (Torres *et al.*, 2018), it is commonly understood as returning 'wildness' to an area through restoring ecological processes to create self-sustaining eco-systems often through the (re-) introduction of select species and removing the need for long-term human management (Pettorelli *et al.,* 2019).

Within Great Britain, several of the vertebrate species lost over the last few centuries are either subject to ongoing reintroduction or being considered for future projects (Harrabin, 2020; Stringer & Gaywood, 2016; White et al., 2015). One such example is the reintroduction of the white stork (*Ciconia ciconia*) in 2016 through a collaborative effort between several conservation charities and landowners known collectively as the White Stork Project (WSP). Before the reintroduction project began, white storks were last recorded nesting in the wild on St Giles Cathedral in Edinburgh in 1416 with some older archaeological evidence to suggest they were also present in southern England (Parker, 1988; Serjeantson, 2010). Today the primary reintroduction site is the Knepp Castle Estate in West Sussex, a once intensively farmed estate which turned to rewilding and eco-tourism site in 2001 when conventional farming was no longer financially viable (Tree, 2018). Although not as immediately impactful as beavers and large herbivores, white storks could be considered a more limited ecosystem engineer, with their large nests providing a nesting habitat for passerines and eventually causing tree mortality (Bocheński, 2005; Jones *et al.*, 1997; Zbyryt *et al.*, 2017) In several European countries the white stork has also been recognised as a flagship species for wetland and grassland conservation in part due to the species' popularity and cultural significance, hence their return may provide an opportunity to reengage the British public with natural world (Kronenberg et al., 2017; Olsson & Rogers, 2009; Thomsen & Hötker, 2013).

The WSP's reintroduction strategy has three elements. Firstly, an open-air pen of roughly 30 flightless individuals is managed to act as an 'anchor' to encourage flying birds to return. Secondly, a group of white storks with the ability to fly were retained in this pen for their first two winters to increase the likelihood of them settling and breeding in the area. Lastly, between 2019-2023, first-year captive-bred individuals are set to be released in late summer to reinforce the population and encourage migratory behaviour. Whilst intensive management is considered at odds with rewilding's goal to create a 'self-willed' ecosystem (Sandom & Wynne-Jones, 2019), it is often required in the initial stages of a reintroduction project to successfully establish small populations as they are more vulnerable to stochastic risks (Frankham, 2010) which can be seen in other rewilding reintroduction projects (Pouget & Gill, 2021).

Since reintroductions carry some level of risk and uncertainty, it can be valuable to understand what parameters need to be met to achieve a self-sustaining population which no longer requires human interventions to thrive. Here we use population viability analysis (PVA) to incorporate biological and environmental variables to predict this novel population's trajectory (Beissinger and McCullough, 2002). Our study aims to (i) discern whether the recently reintroduced British white stork population will be viable in the long term; (ii) assess the impact of different management practices and (iii) migratory behaviour on population growth rates. By studying this reintroduction project in its infancy, imminent threats can be identified, and potential solutions can be explored, improving the chances of reintroduction success.

2.3 Method

Population Viability Analysis

We conducted population viability analysis (PVA) using the software *Vortex 10.5.20* (Lacy, 2019). *Vortex10* is an individual-based simulation model where a population is subjected to a combination of deterministic environmental, demographic and genetic stochastic events based on defined probabilities (Brook *et al.*, 1999). Unless stated otherwise, models were run for 50 years as this time frame would allow for the comparison between the immediate effects of different scenarios while minimising the impacts of errors and uncertainties in the parameter estimates. All models were run for 1000 iterations where extinction was defined as the point when only a single sex remained.

Baseline model

Currently there is minimal data about the British population's demographic parameters, therefore most of the models' inputs were derived from relevant literature (Table 1). PVA's can only be as precise as their input values, and this must be taken into consideration when interpreting their results. To improve the accuracy of model estimates, we only extracted parameter values (mortality and reproductive rates) from papers that fulfilled two criteria. Firstly, only papers with data collected from 1989 onwards were selected to account for the effects of environmental variables on mortality and reproductive rates. For example, during the 20th Century, survival rates of white storks were significantly linked to the amount of rainfall within the Sahel region; this relationship has since weakened (Kanyamibwa *et al.*, 1990; Nevoux *et al.*, 2008a; Schaub *et al.*, 2005). Values produced by older studies would not, therefore, accurately inform models of a present-day British population. Secondly, these populations had to be using a similar migration route to the British storks. European storks migrate using either eastern or western flyways, with the rough dividing line located in central Germany(Shephard et al., 2013). Individuals using the Western Flyway migrate through the Straits of Gibraltar to overwinter in the Sahel region in West Africa which is the route the British storks are taking (authors' unpub. data; Barkham, 2020a). White storks taking this route are anticipated to face similar geographical barriers and risk factors unlike those taking the Eastern Flyway through Istanbul into the wintering areas in East and South Africa which is why eastern populations were excluded (Kanyamibwa et al., 1993)

Literature relating to populations prior to 1989 and/or using the Eastern Flyway were considered for other parameters such as lifespan and maximum brood size (Bocheński & Jerzak, 2006; Hancock et al., 1992; Kaługa et al., 2011).

Table 1. *Vortex10* parameter inputs for the baseline British white Stork population model.

Parameter	Value	Relevant/Supporting literature
Scenario Settings		
Number of iterations	1000	
Number of years	50	
Duration of each year in days	365	
Species Description		
Inbreeding Depression	N/A	
EV correlation between reproduction and survival	0.5	Default value
Reproductive System		
Reproductive System	Long-term monogamy	Barbraud *et al.*, 1999
Age of first offspring	3	Barbraud et al., 1999; Hancock et al., 1992
Max Lifespan	30	Kaluga *et al.*, 2011; Barbraud *et al.*, 1999
Max Age of reproduction	30	Bocheński *et al.*, 2006
Max. broods/year	1	Hancock *et al.*, 1992
Max. progeny/brood	5	Hancock *et al.*, 1992; Hilgartner *et al.*, 2014; Nevoux *et al.*, 2008b
Sex ratio at birth in % Males	50	
Density dependent reproduction	No	
Reproductive Rates		
% adult females breeding	100	Assume all attempt to breed
SD in % breeding due to EV	10	Default Value
Distribution of broods per year/proportion of successful nests	0 – 24% 1 – 76%	Vergara and Aguirre, 2006; Aguirre and Vergara, 2007; Massemin-Challet *et al.*, 2006; Vergara *et al.*, 2006, Wey, 2005
Distribution of offspring per brood	2.75	Aguirre and Vergara, 2007;Vergara *et al.*, 2006; Bossche, 2005;

		Massemin-Challet *et al.*, 2006; Wey, 2005
SD	0.3	
Mate Monopolisation		
% Males in the Breeding Pool	100	Assume all attempt to breed
Initial Population Size		
Initial Population Size	155	Provided by WSP.
Specified Age Distribution	See Table 2	Provided by WSP.
Supplementation		
First year of supplement	1	
Final year of supplement	3	
Supplement from age 0 to 1	12 males, 12 females	Provided by WSP
Carrying Capacity		
K	12,600	(Latus & Kujawa, 2005)
SD in K due to EV	0	

Initial population size

The founder population was derived from three main sources; 74% were wild rescues rehabilitated at Warsaw Zoo Poland, 7% were from Strasbourg, France and the remaining 19% were provided by Cotswold Wildlife Park with mostly Polish origins (Groves, 2021 personal communications). The initial population size entered for the PVA consists of the number of these released white storks and their descendants alive in December 2020, totalling 155 individuals (Table 3). This value does not include the flightless storks, which are restricted to a closed pen area maintained by the WSP, due to their greatly different behaviour and mortality rates.

Reproductive System

White storks are known to have infrequent extra pair copulations (e.g. Turjeman *et al.*, (2016) found that 73.1% of white stork chicks were fully related siblings), and high rates of social monogamy and nest fidelity (Barbraud *et al.*, 1999). Due to the absence of genetic information on the British population, white storks were therefore described in *Vortex10* as having long-term monogamous relationships. Maximum age of breeding for both males and females was set to 30, with one brood per year (Bocheński & Jerzak, 2006). Age of first breeding can vary between and within populations, with recorded cases of 2-year-old storks attempting to reproduce although rarely successfully (Barbraud *et al.*, 1999). For this model the minimum age of successful breading for males and females was set to three years old (Barbraud et al., 1999; Hancock et al., 1992).

Reproductive Rate

It was assumed that 100% of adult females would attempt to breed with a 10% standard deviation (SD) due to environmental variation. Based on means taken from studies which met the aforementioned criteria, weighted based on samples size, it was estimated that 76% of females would successfully fledge their nest at a rate of 2.75 (SD =0.3) fledglings per successful nest (Aguirre and Vergara, 2007; Bossche, 2005; Massemin-Challet *et al.*, 2006; Vergara *et al.*, 2006; Vergara and

Aguirre, 2006; Wey, 2005). Max clutch size was set to five (Hancock *et al.*, 1992; Hilgartner *et al.*, 2014; Nevoux *et al.*, 2008b).

Dispersal

As only one population was modelled in *Vortex10,* dispersal could not be directly considered, nor was there enough data on the British storks to estimate their dispersal rate. Due to their gregarious nature, it is possible some British storks will be attracted to the larger colonies they encounter in Europe, but this information is not yet available, and it will take several years for tracking data on dispersal to be quantified (Bocheński and Jerzak, 2006). Meanwhile, there have been recorded sightings of storks arriving from the European mainland to Britain since 1958, so it is reasonable to assume that the emigration rate may be similar to the immigration rate (Fraser, 2013).

Mortality Rates

Preliminary data from the released individuals indicate that the majority (>70%) migrated following the Western Flyway however, information on survival rates is not yet available (authors' unpub, data). Mortality rates vary significantly with age; first year storks have higher mortality rate due to a lack of experience and less efficient flight strategies (Kanyamibwa et al., 1990; Rotics et al., 2016; Schaub & Pradel, 2004). When exploring the impacts of the current management strategy, it was assumed that all the British storks will take the traditional migration along the Western Flyway towards the Sahel (Kanyamibwa *et al.*, 1990). Both sub-adult (storks aged 1-3) and adult mortality (storks aged 3+) was set at 22.16% (SD due to environmental variation =3) based on the population in the Brouage marshes in west France with rings being recovered in Mali and Uganda (Barbraud *et al.*, 1999; Nevoux *et al.*, 2008b). Juveniles (age 0-1) were assigned a mortality rate of 65.1% (SD due to environmental variation =10) based on a mean derived from Cheng *et al.*, 2019; Flack *et al.*, 2016 and Rotics *et al.*, 2017 and weighted by sample size.

The Impact of Management

Several management options were tested to compare their impacts on the population's growth rate and population size up to 50 years. The management options considered included population supplementation, supplementary feeding/habitat improvement, and provisioning of nesting platforms. The combination and duration of the management options tested are shown in Table 3.

Population Supplementation

The WSP's current management plan is to release a further 24 fledglings over the next three years (see Table 3, 1a). These fledglings are bred by the Cotswold Wildlife Park and due to the success of their captive breeding programme, the authors decided to explore the impacts of increasing the duration of the programme and number of storks supplemented (See Table 3, sceario1b and1c), both realistic in implementation. For all models an equal number of males and females were supplemented.

Provision of Nesting Platforms

The provision of nesting platforms is a common management option in white stork conservation with evidence to suggest that providing platforms in high-quality suitable habitat can increase reproductive success (Hilgartner *et al.*, 2014; Santopaolo *et al.*, 2013). To model the provision of nesting platforms, the percentage of successful breeding females was increased from 76% to 80% in scenario 1d, 1f and 1g. This increase was based on expert experience and considered plausible.

Supplementary Feeding and Habitat Improvement

Studies have shown that access to food supplementation as well as proximity to high-quality habitat can significantly increase the number of fledglings produced (Barbraud *et al.*, 1999; Hilgartner *et al.*, 2014; Massemin-Challet *et al.*, 2006; Tortosa *et al.*, 2003). In scenarios 1e, 1f and 1g, improvement in the breeding habitat quality or food supplementation was represented by increasing the number of fledglings produced per successful nest (Jzm) by 10% to 3.03. This higher productivity value is possible without management interventions; for example, 3.82 fledglings per successful nest has been recorded in the Kizilirmak Delta, Turkey (Yavuz *et al.*, 2012).

Table 2: Exploring different management strategies Scenarios 1a-1g.

Scenario	Years of supplementation	No. individuals supplemented	No. fledglings	Successful nests (%)	Management Description
1a	3	24	2.75	76	Population supplementation
1b	6	24	2.75	76	Population supplementation
1c	6	50	2.75	76	Population supplementation
1d	3	24	2.75	80	Population supplementation, nesting platforms
1e	3	24	3.03	76	Population supplementation, increased food/habitat quality
1f	3	24	3.03	80	Nesting platforms, increased food/habitat quality
1g	6	50	3.03	80	Population supplementation, increased food/habitat quality, nesting platforms

Migratory Behaviour

Whilst white storks are regarded as a migratory species, populations where some individuals overwinter on their breeding grounds can be found in several northern European regions and are expected to grow due to increasingly mild winters and year-round food availability (Gilbert *et al.*, 2016; Massemin-Challet *et al.*, 2006; Olsson, 2007; Schaub *et al.*, 2004). Since migratory behaviour has a large influence of mortality rates, and consequently population growth rates, the relationship between the two were explored (Cheng et al., 2019; Flack et al., 2016; Rotics et al., 2016, 2017). To represent the mortality rate of the non-migratory individuals, values were taken from populations foraging heavily on Portuguese landfill sites year-round and mortality rates for adults and each sub-adult class were obtained (Table 3) (Rogerson *et al.*, 2020). To explore the effect non-migratory behaviour has on the population growth rate, the proportion of non-migratory storks was increased from 0% to 50%. The associated mortality rates entered into *Vortex10* were calculated by taking the previous mean migratory values and those reported by Rogerson *et al.* (2020), weighted based on the proportion of non-migrants being modelled (the exact values entered can be seen in the Supplementary Materials). The mortality rate of juvenile storks (age 0-1) remained at the original value (65.1%) as juvenile storks of non-migratory populations still tend to migrate in their first year (Rogerson *et al*, 2020; Chernetsov *et al.*, 2004).

Table 3: The British white stork initial population size and mortality rates for migratory and non-migratory birds entered into *Vortex10.* EV = environmental variation.

Age	Age distribution of the initial population		Mortality rates (%)		
	Females	Males	Migratory	Non-migratory	±SD due to EV
0-1	17	4	65.1	65.1	10
1-2	26	25	22.16	17.7	3
2-3	7	11	22.16	11.55	3
3+	23	42	22.16	5.4	3

Genetics

The white stork's long-life span and slow generation time may result in deleterious genetic effects initially being hidden within the population. In this instance, the genetic load was represented by lethal equivalents (LE), which expresses the summed selection coefficient of deleterious mutations. For example, if an individual possesses a genetic load of one lethal equivalent, it has a group of deleterious alleles with a summed selection coefficient of one (Bertorelle et al. 2022). If those alleles were all expressed by inbreeding, the fitness of that individual would be e^-1, which is approximately 37% of the fitness of a "perfect" individual without a genetic load. Due to a lack of data on this population's genetic background as well as the impacts of gene flow through dispersal in and out of this population, the models pertaining to management actions and migratory behaviour were set to 0 LE. Additionally, there is evidence to suggest that European white storks did not lose a significant amount of genetic diversity following their 20th Century decline, suggesting that any negative repercussions from inbreeding depression is unlikely to hinder the success of the reintroduction project in the short term (Shephard *et al.*, 2013).

However it is important to consider the genetic background of a reintroduced species due to the potential impacts of founder effect and inbreeding depression (Frankham, 2010; Jamieson, 2011) therefore a separate model was created to explore the relationship between the number of LEs within the population and the mean stochastic growth rate. The number of LEs was increased in increments of 1.25, from 0 to 12.5 based on Frankham's (2010) recommendation that the Vortex 10 default value of 6.29 underestimates the deleterious consequences of inbreeding and should be doubled. The total genetic load that is due to recessive lethal alleles was left at the default value of 50% (Miller & Lacy 2005). The proportion of residents/non-migrants was set to 15% as this was an intermediate value between the 11% and 17% residents reported in German and Swiss populations respectively (Rotics *et al.*, 2017; Schaub *et al.*, 2004). Furthermore, when exploring the impact of non-migratory birds on population growth rate, 15% resulted in a small positive growth rate which we believe would better demonstrate the impact of increasing the number of lethal equivalents within the population. These models were run for 100 years as the long-lived nature of the white stork would mean that genetic impacts may not be visible in the short term.

2.4 Results

The probability of extinction within 50 years for the British population under the WSP's current management strategy (1a) was very low (<1%) with additional management reducing the probability further (Table 4). Models 1a-1c had negative deterministic growth rate whilst 1d-1g had a positive deterministic growth rate. When the population is assumed to fully migratory, maintaining the current WSP management plan (1a) would lead to a negative white stork growth rate (r = -0.0204; Fig 1A, Table 4), suggesting the current management actions would not be sufficient to sustain a viable long-term population. Increasing the length and intensity of the supplementation (1b-1c) would increase population size but would not overcome the negative growth rate once the supplementation ended (r = -0.0185 and -0.0158 respectively; Fig. 1A, Table 4). Combining the current WSP management plan with nest platforms and the associated increase in number of successful nests (1d) would still not be sufficient to overcome the negative population growth rate (r = -0.0116; Fig.1A, Table 4). Alternatively, increasing food/ habitat quality (1e) with the associated higher fledging survival rates would result in a positive growth rate (r =0.0022; Fig.1A, Table 4). Combining both these management options with the current management plan (1f) increased the growth rate further (r =0.0074; Fig1A, Table 4). Combining the greatest length and intensity of population supplementation with nesting platforms and increased food/ habitat quality (1g) resulted in the greatest increase in growth rate and population size after 50 years (r = 0.0104; Fig.1A, Table 4).

Table 4: Population viability model results from *Vortex10* comparing different management strategies on the British white stork (*Ciconia ciconia)*. Det. r = deterministic growth rate. Stoch. r = stochastic growth rate. Exc. supp. years = excluding years where population supplementation occurred; N = population size; PE = probability of extinction in 50 years; SE = standard error

Model	Description	Det. r	Stoch. r ± SE	Stoch. r ± SE exc. supp. years	N after 50 years ± SE	PE (%)
1a	Population supp. (3yrs*24)	-0.0006	-0.0139 ±0.0005	-0.0204 ± 0.0005	103.28 ± 2.51	0.9

1b	Population supp. (6yrs*24)	-0.0006	-0.0076 ±0.0005	-0.0185 ± 0.0005	142.23 ± 3.52	0.1
1c	Population supp. (6yrs*50)	-0.0006	0.0022 ±0.0005	-0.0158 ± 0.0005	222 ± 3.21	0
1d	Population supp. (3yrs*24), nesting platforms (5% increase in successful nests)	0.0074	-0.0053 ±0.0005	-0.0116 ± 0.0005	159.31 ± 3.95	0.3
1e	Population supp. (3yrs*24), increased food/habitat quality (10% increase fledglings)	0.0146	0.0029 ±0.0005	0.0022 ± 0.0005	240.06 ± 5.60	0
1f	Population supp. (3yrs*24), nesting platforms (5% increase in successful nests), increased food/habitat quality (10% increase fledglings)	0.0229	0.0130± 0.0005	0.0074± 0.0005	383.71 ± 9.26	0
1g	Population supp. (6yrs*50), nesting platforms (5% increase in successful nests), increased food/habitat quality (10% increase fledglings)	0.0229	0.0267 ±0.0005	0.0104 ± 0.0005	742.56 ± 15.43	0

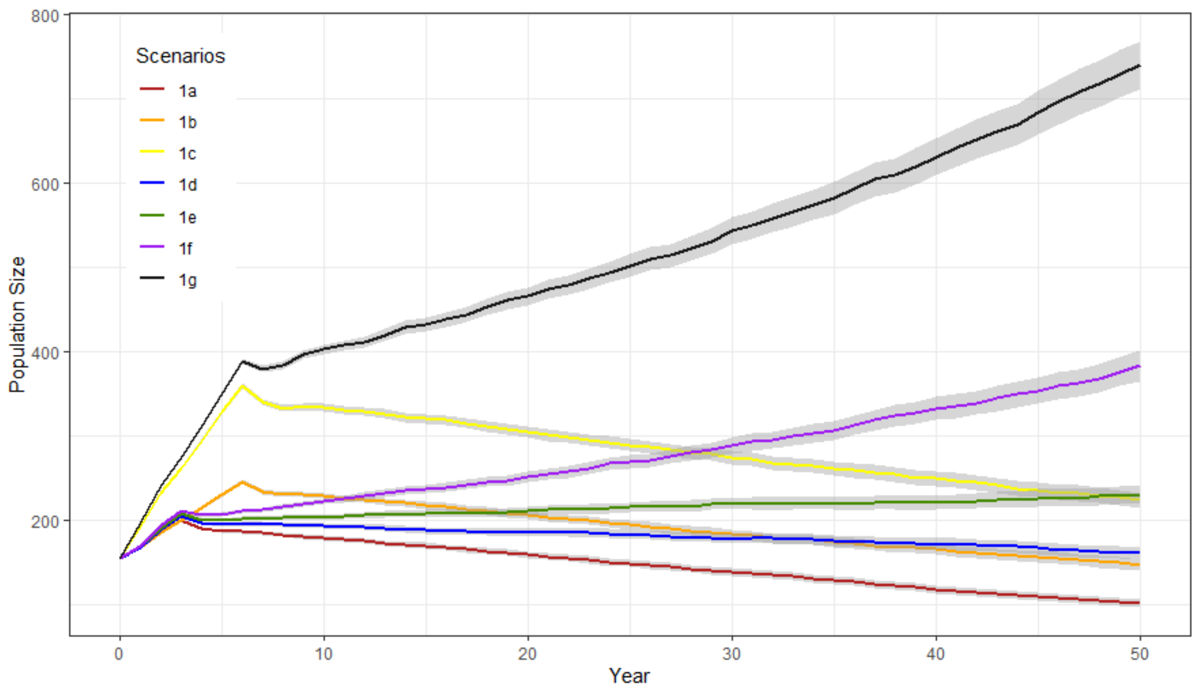

Figure 1: Predicted trends in population size of white storks (*Ciconia ciconia*) in Great Britain over 50 years using *Vortex10* under different management strategies (1a-1g). Initial population size in all scenarios was 155 and a carrying capacity to 12,600. The grey shading represents 95 CI based on the distribution of iterations.

Since the survival of resident birds is higher, there was a positive relationship between the percentage of non-migratory individuals within the populations and mean growth rate (Fig. 2a, Fig. 2b). The deterministic growth rate was only negative when there were no non-migrating individuals in the population (Table 5). With the current management strategy, a positive stochastic growth rates could be achieved if 9% of individuals within the population were non-migratory (Figure 2a, Table 5).

Table 5: Population viability model results from *Vortex10* modelling different proportions of non-migratory individuals in the British white stork (*Ciconia ciconia)*. Det. r = deterministic growth rate. Stoch. r = stochastic growth rate. Exc. supp. years = excluding years where population supplementation occurred. N = population size. PE = probability of extinction of the population in 50 years. SE = standard error

Percentage of non-migrants (%)	Det. r	Stoch. r ± SE	Stoch. r ± SE exc. supp. years	N (extent) after 50 years ± SE	PE (%)
0	-0.0006	-0.0143± 0.0005	-0.0208± 0.0005	103.60±2.58	0.6
1	0.0009	-0.0130± 0.0005	-0.0193± 0.0005	112.86±2.91	0.8
2	0.0024	-0.0106± 0.0005	-0.0166± 0.0005	120.06±2.75	0.4
3	0.0038	-0.0092± 0.0005	-0.0155± 0.0005	131.47±3.11	0.4
4	0.0052	-0.0075± 0.0005	-0.0138± 0.0005	141.67±3.33	0.2
5	0.0067	-0.0049± 0.0005	-0.0110± 0.0005	160.99±3.92	0.1
6	0.0082	-0.0034± 0.0005	-0.0095± 0.0005	168.93±3.73	0.3
7	0.0096	-0.0017± 0.0005	-0.0078± 0.0005	183.07±4.20	0
8	0.0110	-0.0001± 0.0005	-0.0058± 0.0005	199.57±4.47	0
9	0.0125	0.0022± 0.0005	-0.0038± 0.0005	223.02±5.02	0.1
10	0.0139	0.0038± 0.0005	-0.0022± 0.0005	239.72±5.39	0.2
11	0.0153	0.0053± 0.0005	-0.0006± 0.0005	258.99±5.58	0.1
12	0.0168	0.0072± 0.0005	0.0014± 0.0005	280.02±6.32	0
13	0.0182	0.0085± 0.0005	0.0027± 0.0005	303.97±7.08	0.2
14	0.0197	0.0103± 0.0005	0.0047± 0.0005	325.20±6.86	0
15	0.0211	0.0119± 0.0005	0.0062± 0.0005	352.37±7.78	0
20	0.0282	0.0201± 0.0005	0.0144± 0.0005	523.02±11.12	0
25	0.0353	0.0279± 0.0004	0.0224± 0.0005	751.90±15.13	0
30	0.0424	0.0369± 0.0004	0.0318± 0.0004	1179.81±25.41	0
35	0.0494	0.0446± 0.0004	0.0396± 0.0004	1727.50±35.4	0
40	0.0563	0.0519± 0.0004	0.0471± 0.0004	2436.27±47.06	0
45	0.0633	0.0597± 0.0004	0.0549± 0.0004	3537.38±64.14	0
50	0.0703	0.0665± 0.0004	0.0618± 0.0004	4919.97±81.55	0

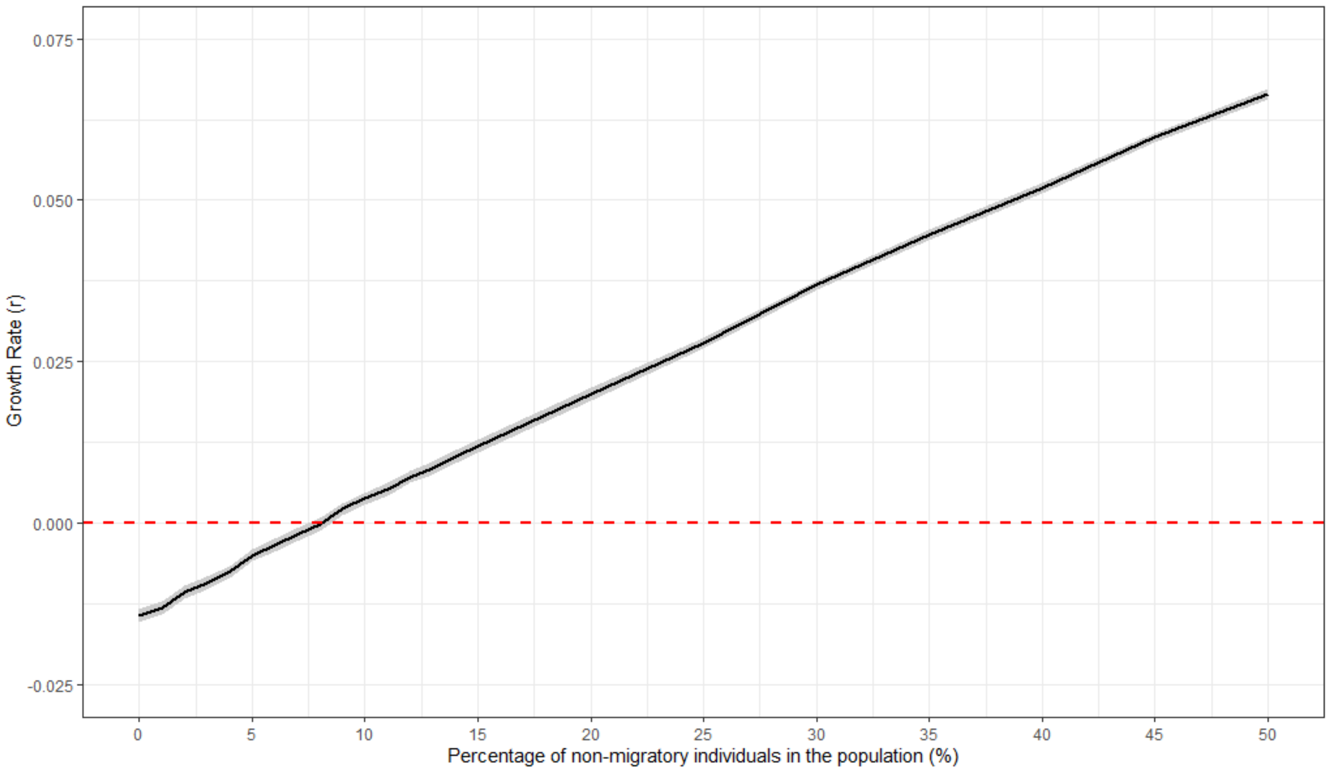

Figure 2a: The relationship between the percentage of non-migratory/resident white stork (*Ciconia ciconia*) overwintering in Great Britain and the mean stochastic growth rate of the population across all years. Models were produced using *Vortex10* and were run for 50 years and 1000 iterations. Initial population size in all scenarios was 155 and a carrying capacity to 12,600. The grey shading represents 95% CI from the distribution of values from all iterations.

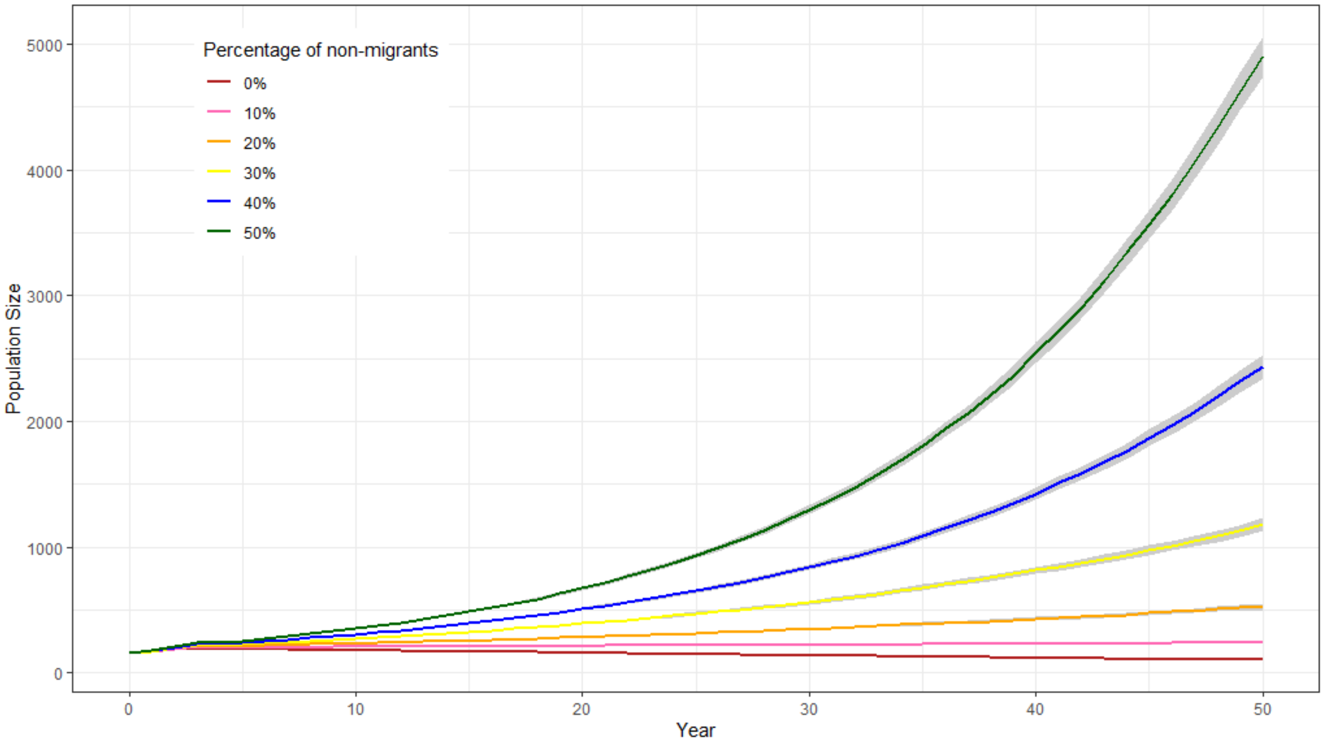

Figure 2b: Predicted trends in population size of white storks (*Ciconia ciconia*) in Great Britain over 50 years using *Vortex10* where different percentages of non-migratory individuals within the population were modelled. Initial population size in all scenarios was 155 and the carrying capacity was set to 12,600. The grey shading represents 95% CI from the distribution of values from all iterations.

Within the genetics model There was a negative correlation between the number of lethal equivalents and stochastic population growth (Fig. 3). Within a population that contains 15% non-migratory birds, negative population growth was observed when the number of lethal equivalents reached 5 (r = -0.0016; Fig. 3) when the model is run over 100 years. The population's probability of extinction also increased with the number of lethal equivalents, with over a quarter (25.7%; Table 6) of iterations going extinct at the highest value of 12.5.

Table 6: Population viability model results from *Vortex10* modelling different numbers of lethal equivalent in the British white stork (*Ciconia ciconia)*. Det. r = deterministic growth rate. Stoch. r = stochastic growth rate. Exc. supp. years = excluding years where population supplementation occurred. N = population size. PE = probability of extinction of the population in 100 years. SE = standard error

Lethal Equivalent	Det. r	Stoch. r	N (extent) after 100 years ± SE	PE (%)

0	0.0211	0.0099±0.0003	719.56±25.53	0.9
1.25	0.0211	0.0065±0.0003	583.25±24.16	2
2.5	0.0211	0.0037±0.0003	482.44±19.00	2.2
3.75	0.0211	0.0009±0.0003	407.18±16.88	4.1
5	0.0211	-0.0016±0.0003	340.97±14.03	5.9
6.25	0.0211	-0.0051±0.0003	269.16±12.41	8.3
7.5	0.0211	-0.0078±0.0004	250.32±12.75	11.7
8.75	0.0211	-0.0105±0.0004	210.45±10.73	14.9
10	0.0211	-0.0136±0.0004	191.76±11.25	17.7
11.25	0.0211	-0.0153±0.0004	168.37±11.36	20.1
12.5	0.0211	-0.0178±0.0004	149.01±9.67	25.7

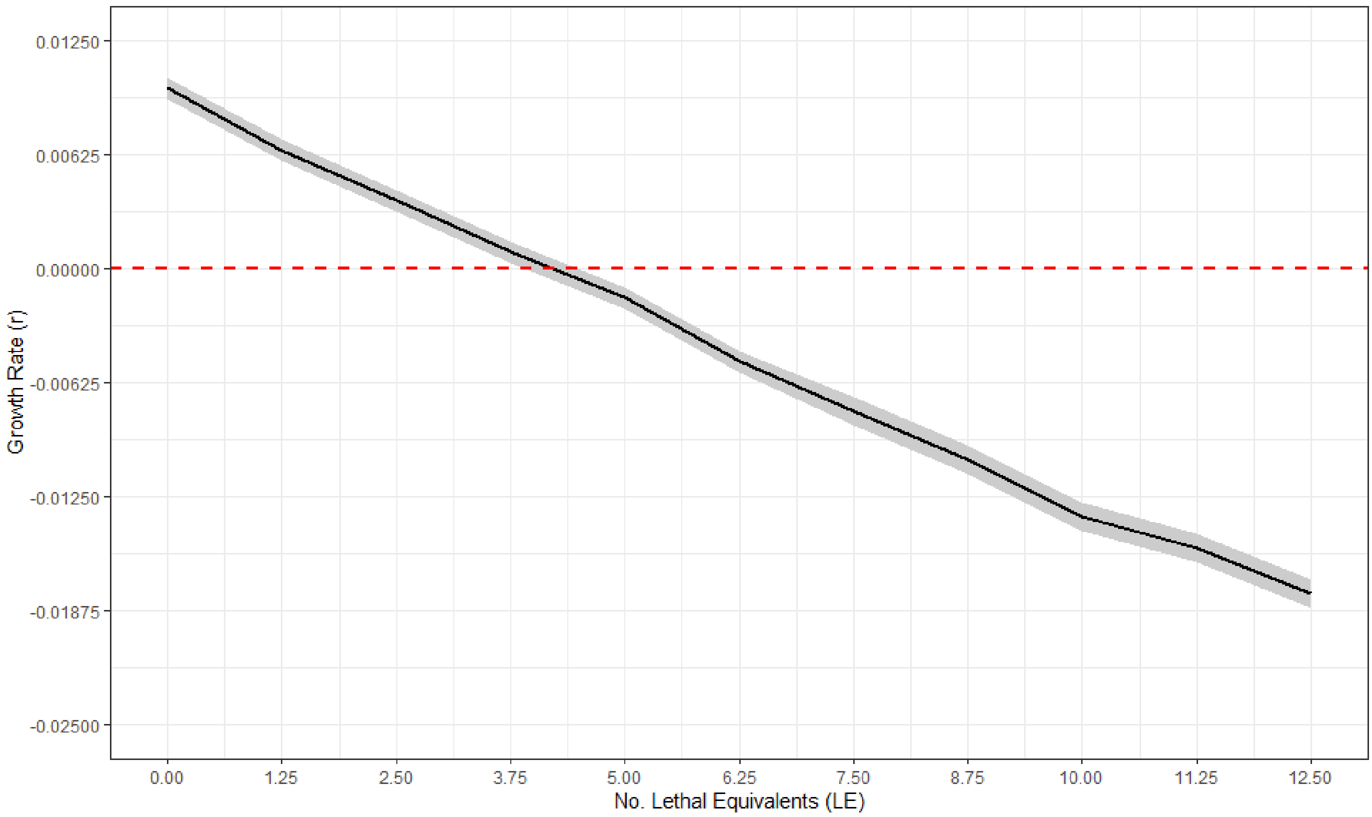

Figure 3: The relationship between the number of lethal equivalents (LE) and the mean stochastic growth rate of the British white stork (*Ciconia ciconia)* population where 15% of the population were residents. Models were produced using *Vortex10* and were run for 100 years and 1000 iterations. Initial population size was set to 155 with a carrying capacity of 12,600. The grey shading represents 95% CI from the distribution of values from all iterations.

2.5 Discussion

This study has shown that under the current management strategy, PVA models predict a decline in the population size if the entire British white stork population chose to migrate along traditional routes. However, the decline would be slow, with only a 0.9% chance of the population going extinct within 50 years. Supplementing the population with a greater number of juveniles, across a longer time period, did further reduce the probability of extinction and delayed when the population would start to decline but could not prevent it entirely. Instead, management actions which increased reproductive output were generally more effective. The provision of suitable nesting sites reduced the rate of the decline compared to the current management strategy, whilst providing additional food or improving habitat quality did achieve a positive growth rate. Combining all the management actions achieved the greatest positive growth rate. Alternatively, if a minimum of 9% of adults overwintered in the UK as residents, additional management would not be required due to the associated lower mortality rate with this behaviour. Lastly, as the number of lethal equivalents in the population increased, the populations growth rate decreased and the probability of extinction increased. Overall, this study suggests a promising future for white storks in the UK, and hopefully this reintroduction will follow upon the successes of previous white stork reintroductions undertaken across western Europe (Thomsen & Hötker, 2013).

Many migratory birds, including white storks, are exposed to an array of threats whilst migrating, including hunting pressure and electrocution from overhead powerlines (Cheng *et al.*, 2019; Kaługa *et al.*, 2011; Klaassen *et al.*, 2014; Lok *et al.*, 2015; Raine *et al.*, 2016). Whilst actions such as modifying electrical poles are being implemented to minimise these risks and the associated mortality (Kaługa et al., 2011), local management actions which improve reproductive output can also be used to counter high mortality rates (Schaub *et al.*, 2004). Ensuring access to reliable food supplies close to the nesting sites, from either anthropogenic or natural sources, can be an important factor for the successful rearing of fledglings as the foraging range of breeding storks is restricted in the chick rearing period (Hilgartner *et al.*, 2014; Massemin-Challet *et al.*, 2006; Tortosa *et al.*, 2003). Food provisions can also minimise detrimental impacts of heavy rainfall in the early chick rearing period when chicks are particularly vulnerable and this stochastic mortality due to extreme weather may increase in frequency with climate change (Kosicki, 2012; Olsson, 2007; Tobolka et al., 2015).

If the British population did require intensive prolonged management, such as directly providing food to prevent a decline, the reintroduction is unlikely to be considered a success (IUCN, 2013). Furthermore, such human intervention is often at odds with the values of rewilding, of which this particular project is associated with due to the primary reintroduction site being located on the Knepp Castle Estate (Perino *et al.*, 2019; White Stork Project, 2021a). However, this study shows that a positive population growth rate could be achieved if a small proportion of adults overwintered in the

UK as residents due to the lower mortality rate associated with avoiding migration. The trend for white storks to take shorter migrations or remain at their breeding grounds all year has been increasing in the past few decades, particularly around the Iberian Peninsula where large proportions of the population stay year round (Catry *et al.*, 2017; Cuadrado *et al.*, 2016). This is thought to be due to milder climates and the emergence of reliable year found food sources such as landfills and invasive crayfish (Archaux *et al.*, 2004; Cheng *et al.*, 2019; Ferreira *et al.*, 2019; Gilbert *et al.*, 2016).

Unlike in Portugal where studies have reported 75% of the population remaining all year round (Andrade *et al.* submitted), this study only modelled the influence of residency in the UK up to 50% of the population, for although white storks can tolerate colder temperatures, the associated lack of consistent food can make year round residency difficult without human intervention (Mata *et al.*, 2001). This was seen during the early stages of white stork reintroductions in Sweden and Switzerland, where individuals were kept in captivity until they reached sexual maturity to improve their probability of survival, but subsequently did not exhibit migratory behaviour once released and had to rely on feeding stations in order to survive winter (Olsson, 2009; Schaub *et al.*, 2004). It is interesting to note that the morality rates calculated for the resident birds in Switzerland were similar to the values adopted by this study which were derived from a Portuguese population residing on a landfill (Schaub *et al.,* 2004; Rogerson *et al.,*2020). This implies that if a reliable food source is available resident, British storks may possess mortality rate despite the difference in climate.

The UK has considerably milder winters in comparison to Sweden and Switzerland, so it is not expected that food supplementation would be necessary to support an overwintering population (Gow *et al.*, 2016). It is also possible that as the British stork population grows it may start utilizing landfills, as seen across Europe, which will providing extra resources for overwintering individuals (Massemin-Challet *et al.*, 2006). However, municipal biological waste (of which food waste is contained) has been steadily decreasing over the past decade across the UK and Europe more wildly and is anticipated to continue in line with an EU waste legislation thus minimising landfills effectiveness as a food source (DEFRA, 2021; Wang *et al.*, 2020).

In terms of non-anthropogenic food sources, there may be sufficient high-quality semi-natural habitat to support overwintering individuals as is the case for other wetland species in Britain (Amaral-Rogers, 2021). Storks are oppurtunistice feeders, and whilst the composition of their diet varies depending on the availibity, it often consists of insects, small mammals, and worms (Antczak et al., 2002; Chenchouni, 2017). However, across the 20th Century, many of the tradtional white stork breeding habiats such as wetlands, pastures and wet meadows were converted for use in intemsive argicutltre, thus greatly reducing food aviability which in turn contributed the significant population decline across mnay western European white stork populations (Donald et al., 2001; Luthin, 1987; Verhoeven, 2014). Eliminating the causes of past declines is vital for reintroductions to be successful, and there are several examples of habitat restoration projects across Europe with the aim of supporting white stork populations (ESVN, 2021; IUCN, 2013; Thomsen & Hötker, 2013). There is also some evidence to suggest that the white stork is an effective indicator species for farmland biodiversity (Tobółka *et al.*, 2012). Since the UK is a biodiversity deprived country with persistent declines in farmland and wetland bird populations, the reintroduction of the white storks is likely to spark high interest and levels of engagement (Briggs, 2021; DEFRA, 2020; Newton, 2004; Robinson & Sutherland, 2002).The restoration of wetlands and pastures and associated biodiversity would not only support white storks over winter but could also improve reproductive outputs in the spring and summer (Carrascal *et al.*, 1993). Research on how UK storks are currently utilizing the landscape, both during the breeding and non-breeding seasons, could help focus such efforts and aid in the efficient allocation of conservation resources (Olsson & Rogers, 2009).

This study uses a modelling approach to provide guidance for conservation management however there are several parameters that could be improved to increase the PVA's performance as a management tool. Firstly, a significant limitation of these models is the lack of consideration for dispersal behaviour, a highly influential parameter for which data is not yet available. The majority of the population are still sub-adults which are known to show more exploratory behaviours that breeding adults, and so it may still be a few years before the general trend in dispersal is understood (Chernetsov *et al.*, 2006; Itonaga, 2009; Vergara *et al.*, 2007). In white storks, natal dispersal occurs more commonly than breeding dispersal, and they more often disperse along their migration routes, although the availability of suitable nesting habitats is also influential (Chernetsov *et al.*, 2006; Itonaga *et al.*, 2010; Rojas *et al.*, 2016, Ječmenica and Kralj, 2017). This suggests that some of the storks released in the UK may be attracted to joining the larger French and Iberian colonies that are found along the Western Flyway which would reduce the British population's growth rate (Ieronymidou et al., 2016; Thomsen & Hötker, 2013). However, the rate of this dispersal is difficult to predict as the influence of density effects varies across different populations (Itonaga, 2009; Rojas *et al.*, 2016). Furthermore some loss from dispersal could be mitigated by incoming birds; both the British and Swedish populations have attracted immigrating storks even though the populations are small and at the edge of the species' range (Olsson, 2013; White Stork Project, 2021b). As the British population ages and gains higher numbers of breeding adults, the impact of the population's dispersal patterns will become clearer and should be incorporated to produce a more robust model.

Additionally, genetic variables were only lightly explored within this study due to a lack of data on the genetic diversity of the founder population, their reproductive skew and the mitigating influence of gene flow through the supplementation of individuals and dispersal behaviour which all would affect the models' outputs (Heber et al., 2013; Jamieson, 2011; Le Gouar et al., 2008). It is concerning that in a population where 15% of individuals are non-migratory, it only required 5 lethal equivalents to produce a negative growth rate highlighting the significant negative impact inbreeding depression can have on small populations. Hence, we strongly recommend further research into the white stork's genetic load so this risk can be better modelled and understood.

Even with the uncertainty associated with the aforementioned population parameters, this reintroduction project has a high probability of creating a viable British white stork population, particularly if a residential population forms. Many of the models' weaknesses are due a lack of data on this novel population on account of the reintroduction project's infancy. We recommend that as more data on this population becomes available, the models' inputs should be updated and developed to improve their accuracy and effectiveness in assisting in with management decisions.

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2.7 Supplementary materials

The exact mortality rates entered into *Vortex10* based on the percentage of non-migratory individuals with the population.

Table 1: The mortality rates of each age class entered into Vortex10 based on the percentage of non-migratory individuals within the population being modelled

Non-migratory (%)	0-1	1-2	2-3	3
0	65.1	22.16	22.16	22.16
1	65.1	22.12	22.05	21.99
2	65.1	22.07	21.95	21.82
3	65.1	22.03	21.84	21.66
4	65.1	21.98	21.74	21.49
5	65.1	21.94	21.63	21.32
6	65.1	21.89	21.52	21.15
7	65.1	21.85	21.42	20.99
8	65.1	21.80	21.31	20.82
9	65.1	21.76	21.21	20.65
10	65.1	21.71	21.10	20.48
11	65.1	21.67	20.99	20.32
12	65.1	21.62	20.89	20.15
13	65.1	21.58	20.78	19.98
14	65.1	21.54	20.67	19.81
15	65.1	21.49	20.57	19.65
20	65.1	21.27	20.04	18.81
25	65.1	21.05	19.51	17.97
30	65.1	20.82	18.98	17.13
35	65.1	20.60	18.45	16.29
40	65.1	20.38	17.92	15.46
45	65.1	20.15	17.39	14.62
50	65.1	19.93	16.86	13.78

3. Chapter 2: Modelling the habitat foraging preferences of white storks

3.1 Abstract

Reintroductions play an important role in conservation management as they provide a means to increase biodiversity and aid in restoring ecosystem function to an area. However, their success rates can be low due to insufficient knowledge of the species' habitat requirements at the new reintroduction sites. Habitat suitability models created in the early stages of a species reintroduction can provide a way to identify key environmental variables that influence an area's suitability and locate high-quality habitats which can be created or incorporated into management strategies to increase the likelihood of a successful reintroduction.

Following the recent reintroduction of the white stork to the UK, we conducted the first study to identify which habitat variables are associated with the population's foraging behaviour during the breeding season when the presence of high-quality habitat is crucial for reproductive success. After collecting the field data, habitat-suitability models were developed using generalised linear models at both local (100m resolution) and micro (10m resolution) scales to understand the spatial scale at which potential management measures would need to be implemented. The local scale model was then used to map the availability of favourable areas around white storks' reintroduction site.

White storks were shown to prefer foraging in open areas close to their nests and water. White stork presence was also positively correlated to an open-air pen where injured storks were fed. Grass height was only identified as a significant explanatory variable at the micro-scale, with white storks preferring areas with shorter grass. Disturbance by walkers and the number of livestock were not influential at their current levels. These models can support and inform further white stork reintroductions.

3.2 Introduction

Over the course of the 20th Century, agricultural intensification has dramatically altered the European landscape through the reduction in uncultivated areas, changes in crop rotations and the widespread uptake of pesticides and fertilizers (Donald et al., 2001). This resulted in dramatic declines in biodiversity as many species which once thrived in agricultural environments experienced range reductions, decreases in population size and/or local extinctions due to the loss of high-quality habitats and food (Donald et al., 2001; Henle et al., 2008; Newton, 2004). In response to this decline, Europe has undertaken many forms of conservation and habitat restoration projects in attempts to reverse this biodiversity loss (Bullock et al., 2011; Lamers et al., 2015; Ledoux et al., 2000). One such method is 'rewilding' which often relies on the reintroduction of lost species to restore ecological processes and services to an area to create a 'wild' self-sustaining eco-system which requires minimal human management (Carver et al., 2021; Pereira & Navarro, 2015; Pettorelli et al., 2019).

However, reintroductions are inherently challenging, resource heavy and the outcomes can be difficult to predict (Ewen et al., 2012; Taylor et al., 2017). Large 'wilderness' areas are rare, particularly in western Europe, and if a reintroduction is successful the species will likely migrate out of the reintroduction site as the population density increases (Mueller et al., 2020; Yott et al., 2011) Whilst some species are able to adapt to anthropogenic landscapes (Cretois et al., 2021) it is highly beneficial for reintroduction projects to identify which environmental variables most affect the suitability of the landscape in which the reintroduction is to occur through the use of habitat suitability models (Cook et al., 2010; Nüchel et al., 2018; Paraskevopoulou et al., 2022). For example, inadequate food supply can significantly impact survival and breeding success (Armstrong et al., 2007), and human disturbance can drive individuals out of reintroduction sites into less suitable areas or lead to nest desertion (Larkin et al., 2004; Margalida et al., 2003). Additionally, when such variables are known, habitat suitability models can be developed to identify other high-quality areas within the region which may be utilized as the population continues to grow, although it is also important to consider the spatial resolution through which habitat suitability models are produced as patterns and relationships visible at one scale may go undetected at another (Chave, 2013; Guisan et al., 2017; Guisan & Zimmermann, 2000). Such information can then be used to inform future management strategies or development plans within and surrounding the reintroduction site to increase the probability of the reintroduction's success (La Morgia et al., 2011; Olsson & Rogers, 2009).

White storks (*Ciconia ciconia*) are a long-distance migratory bird that experienced significant population declines and local extinctions across western Europe when many of their traditional breeding habitats, including grasslands, wetlands, pastures, and wet meadows, were converted for use in intensive agriculture (Donald et al., 2001; Luthin, 1987; Verhoeven, 2014). In response to this decline there have been several successful reintroduction and habitat restoration projects across Europe with the aim re-establish populations of this culturally significant and charismatic bird (ESVN, 2021; Schaub et al., 2004; Thomsen & Hötker, 2013).

Within the UK the reintroduction of the white stork commenced in 2016, with the primary reintroduction site located on the Knepp Castle Estate in West Sussex, a once intensively farmed estate which turned to rewilding and eco-tourism site in 2001 when conventional farming was no longer financially viable (Tree, 2018). Understanding how the white stork population is utilizing this unique habitat is valuable especially in the early stages of the reintroduction, particularly during the nesting season as white stork's foraging range is greatly reduced to a 5km radius around the nest (Tryjanowski & Kuźniak, 2002; Zurell et al., 2015).

This study aimed to a) identify which habitat variables are associated with white stork foraging behaviour b) use these variables to produce a habitat-suitability model and map the availability of favourable areas around white storks' reintroduction sites and c) examine habitat-suitability at local and micro-habitat scales to understand the spatial scale at which management measures need to be implemented.

3.3 Method

Field methods and study species

Field data was collected from the Knepp Castle Estate and the neighbouring village of Shipley located in West Sussex, UK (Fig. 1). The estate predominantly consists of scrubby grassland with patches of woodland which are grazed by free moving livestock and deer. The Shipley area mostly consists of smaller meadows and pastures containing horses and cows, as well as gardens and woodlands. Lakes, ponds and streams are also present.

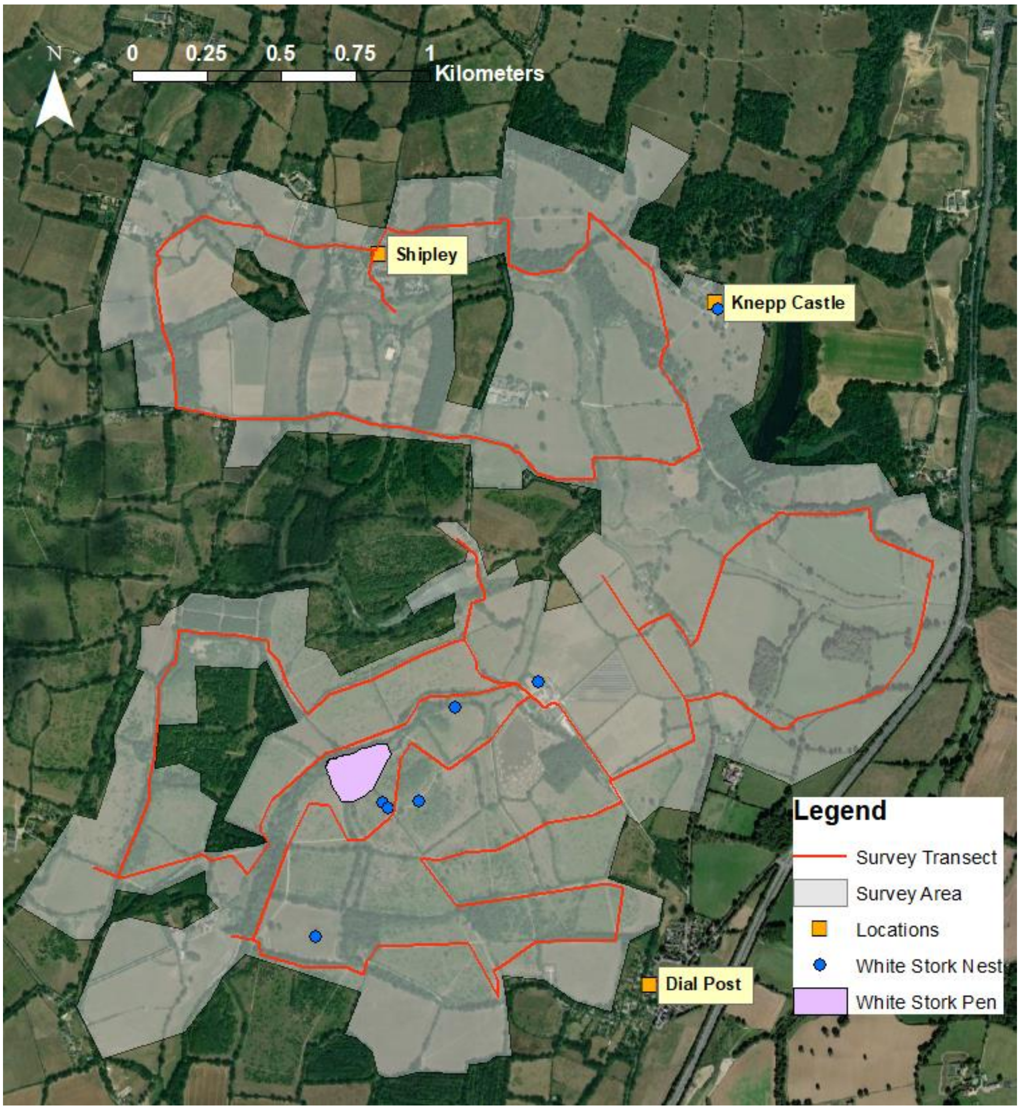

Figure 1: Area surveyed by transects to detect foraging storks and the location of active white stork nests in 2021.

The white stork reintroduction project began in 2016 through a collaborative effort between several conservation charities and landowners known collectively as the White Stork Project (WSP) (White Stork Project, 2021a). The founder population was sourced from three locations; 74% were wild rescues rehabilitated at Warsaw Zoo, Poland, 7% were from Strasbourg, France and the remaining 19% were provided by Cotswold Wildlife Park with mostly Polish origins (Groves, 2021 personal communications). Roughly 30 flightless individuals are held in an open-air pen to act as an 'anchor' to encourage flying white storks to return. These flightless storks are fed daily and the flying individuals including those breeding have been seen taking advantage of food provided (Groves, 2021 personal communications). In 2020 there were 2 breeding pairs nesting on the estate which increased to 7 breeding pairs in 2021 (Figure 1).

A 20km transect was defined to capture habitat utilization by the white storks. This transect was divided into 3 segments, covering portions of the Knepp Castles Estate's lower block and middle block, as well as the village of Shipley, measuring 10.5km, 4.2 km and 5.7 km respectively with minor deviations to maintain visibility as vegetation height varied across the survey period. The transect was walked at a steady pace and was formed of a mixture of public footpaths, country roads and off footpath portions with the permission of the landowners. The entire survey area totalled 5.41km^2. The survey period lasted 9 weeks, starting at the beginning of May and ending the first week of July resulting in a total of 18 transects with a total of 107 sightings of foraging white storks across that time period.

The presence of white storks exhibiting foraging behaviour was recorded along each transect. If more than one stork was observed foraging in the same area it was still recorded as one presence point. Any sightings of white storks flying overhead or perched in trees or nests were not included, as well as the injured flightless storks that permanently resided within the open-air pen. Habitat variables were characterised based on existing information from remote sensing datasets and further validated with field surveys. The number of large herbivores (cows, horses, ponies, sheep and deer) were recorded and converted into livestock units (Table 1).

Table 1: Livestock unit conversions

Animal	Livestock Unit	Source
Cow	1	(Natural England, 2013)
Horse	1	(Natural England, 2013)
Pony	0.8	(Natural England, 2013)
Pig	0.3	(Eurostat, 2022)
Lowland sheep	0.12	(Natural England, 2013)
Red deer	0.3	(Chapman, 2017)
Fallow deer	0.15	(Chapman, 2017)
Roe deer	0.08	(Chapman, 2017)

Grass height was recorded by taking ten random samples in key fields and calculating a mean height (cm). Measurements were taken at least 5 metres away from a footpath edge to avoid the impact of trampling by walkers. In areas which were visible by not accessible, vegetation height was estimated. These values were then placed into the following categories: 1 for 0-10cm; 2 for 11-20 cm; 3 for 21-30 cm; 4 for 31-40 cm; 5 for 41-50 cm; 6 for 51-60 cm; 7 for 61-70 cm; 8 for 70+ cm. For each of the 3 segments, the mean number of walkers encountered along during a survey was also recorded.

Habitat suitability models at local and micro-scales

Two habitat suitability models were built, the first at a local scale and the second at a micro. The local scale analysis enables the visualisation of the habitat suitability index of the whole area surveyed whilst the micro scale analysis (10m resolution) focuses on the individual bird that has been observed along the transect and enables a better understanding of the micro-habitat characteristics that the white storks are selecting.

For the local scale analysis, a 100m^2 grid (British National Grid) was transposed across the survey area. Each grid square was assigned either '1' or '0' to indicate stork presence or absence respectively. In total 39 out of the 541 grid squares surveyed had a white stork present. To indicate the presence of the white stork pen (Fig. 1) A grid square would be assigned as '1' if 90% of the grid square was covered by the stork pen and '0' otherwise. The area of a grid square containing grassland, pasture or meadow was calculated based on the digitised map; these values were then transformed using the arcsine square root transformation. Distance variables were also calculated between the centroid of the grid square to the edge of the relevant feature (see Table 2 for more information).

Table 2: Independent variables considered for analysis in a grid-based model

Variable	Description	Unit
White stork pen	White stork pen covers 90% of a grid sqaure	0/1
Livestock Units	The mean number of livestock units	n/a
Distance to nest	Distance from grid centroid to the nearesr nes	m
Distance to water	Distance from grid centroid to the nearest body of water	m
Grass Cover	Area of the grid square containing grassland,pasture or meadow	m^2
Grass Height	Categories of mean height of grass	1-8
Disturbance Index	Distance from grid centroid to closest footpath*mean disturbance rate of closest footpath*-1.	n/a

To incorporate the impact of human disturbance the average number of walkers seen on footpaths for each of the 3 segments were recorded and divided by the length of that segment to deduce a mean disturbance rate for each segment. The distance from a centroid to the nearest footpath was calculated and multiplied by the mean disturbance rate and then inversed so grid squares which were further away from the footpath had lower values to represent a lower intensity of disturbance to create a disturbance index.

For the micro-habitat scale model we analysed foraging choices at a resolution <10m. For each sighting, 10 random points were generated within 500 from to represent pseudo absences. If the random points were located in habitats not be accessible to the storks or suitable for foraging, the points were re-generated.

What was deemed suitable or unsuitable was based on the authors knowledge of feasible foraging habitat and supported by wider literature of stork foraging behaviour (Table 3) (J. C. Alonso et al., 1991; Carrascal et al., 1993; Gilbert et al., 2016; Olsson & Rogers, 2009) For example, whilst storks are often associated with wetland environments they do not commonly forage in the deep water bodies within the Kneep Estate, and more commonly use the water edge (Tryjanowski et al., 2005;

Shulz, 1998) . The white stork pen observations were excluded as in this case we were interested in foraging behaviour in natural habitats rather than supplementary sources.

Table 3: Landcover categories and their foraging suitability

Grassland	Suitable
Scrub	Unsuitable
Woodland	Unsuitable
Pasture	Suitable
Water	Unsuitable
Reed bed	Suitable
Sports pitch	Unsuitable
Garden	Suitable
Buildings	Unsuitable
Hard standing	Suitable
Natural path	Suitable
Metal path	Suitable
Solar panel field	Unsuitable
Other	Suitable

Each presence location and associated pseudo-absence points were assigned the mean height of the grass at that presence point's location during the week of surveying it was recorded in. Distance variables were calculated between each point and the edge of the relevent feature. Mean livestock units were derived from the grid square as seen in the local scale model. Disturbance was also calculated by the same method and the local scale model to form a disturbance index (see Table 4 for more information).

Table 4: Independent variables considered for analysis in a point-based model

Variable	Description	Unit
Livestock Units	The mean number of livestock units in the grid square the point resides in	n/a
Distance to nest	Distance from point to the nearest nest	m
Distance to water	Distance from point to the nearest body of water	m
Grass Height	Mean height of grass during that week of surveying	1-8
Disturbance Index	Distance from a point to closest footpath*mean disturbance rate of closest footpath*-1.	n/a

Data analysis and visualisation of results

Generalised linear models were used to determine the storks' habitat suitability models at the two scales (local and micro). To avoid multicollinearity, independent variables were tested for pair-wise correlations using Spearman's rho. Independent variables were scutinised for their level of correlation and all variables met the correlation threshold for inclusion in the modelling procedure (correlation coefficient <0.60). R-studio version 3.6.2 was used to run statistical analysis and construct the models. We used the 'drege()' tool in the 'MuMin' package for both the local- and the micro-scale models, to identify the combination of variables that produced the optimal models based on the Akaike's information criterion modified for small sample size (AICc) (Burnham and Anderson, 1998). All models within ΔAICc≤ 2 are presented and discussed. The 'predict' function was used to generate the white stork probabilities of occurrence for each model within ΔAICc≤ 2 and the average of the predicted values was used to generate, using ArcMap 10.6.1, the final habitat suitability map at local scale.

Probability of occurence values were divided into 4 categories representing different levels of habitat suitability. The first threshold was determined based on the value that optimised sensitivity and specificity of the model. The remaining probability values were split into 3 equal percentiles designated low, medium and high suitability.

3.4 Results

Table 5: Environmental variables measured (mean ± standard deviation) in the entire study area (n=541) and in the grid cells (100 m^2 grid scale) where storks were recorded (n=39).

Variable	Mean of entire study area ± SD	Mean in areas with stork presence
Livestock Units	0.152 ± 0.383237	0.175 ± 0.343249
Distance to nest	675.489 ± 241.0175	309.144 ± 414.700
Distance to water	175.091± 167.445	116.482 ± 146.531
Grass cover	7791.507 ± 2535.976	8205.215± 2195.409
Grass height category	3 ± 1.856	2 ± 1
Disturbance Index	1.96 ± 0.341	1.86 ± 0.556

White storks where present in 39 out of 541 the 100m^2 grid squares. After undergoing the AICc based model selection for the local spatial scale, the best model (G1) contained the explanatory variables 'distance to water' and 'distance to nest', which were both negatively associated with white stork presence, as well as the explanatory variables 'grass area' and 'presence of the white stork pen', which we positively correlated (Table 6).

There were two further models which were also within ΔAICc≤ 2 of model G1. In model G2 there was the addition of mean livestock units which had a negative relationship with white stork presence whilst in model G3 the variable grass height was included which also had a negative relationship. However, both these variables had standard deviations greater than their associated coefficients so meaningful interpretations of these variables could not be made and therefore were not graphically represented. The explanatory variable 'disturbance index' was not retained in the model selection process.

Table 6: Three best generalised linear models (∆AICc<2) and their coefficients (SD = standard deviation) explaining variation in the probability of white stork presence. Log-likelihood function (logLik), Akaike information criteria with correction for small sample sizes (AICc), AICc differences (∆i) and Akaike weights. SD = standard deviation

Model	Intercept	Grass Area ± SD	Pen ± SD	Grass Height ± SD	Livestock Units ± SD	Distance to nest ± SD	Distance to water ± SD	logLik	AICc	∆i	Akaike weight
G1	-2.264 ± 0.883	1.621 ± 0.707	3.102 ± 1.23			-0.004 ± 0.001	-0.004 ± 0.002	-108.832	227.8	0	0.212
G2	-2.255 ± 0.883	1.702 ± 0.716	3.056 ± 1.232		-0.309 ± 0.456	-0.004 ± 0.001	-0.004 ± 0.002	-108.583	229.3	1.55	0.098
G3	-2.143 ± 883	1.621 ± 0.705	3.091 ± 1.228	-0.060 ± 0.153		-0.004 ± 0.001	-0.004 ± 0.002	-108.756	229.7	1.89	0.082

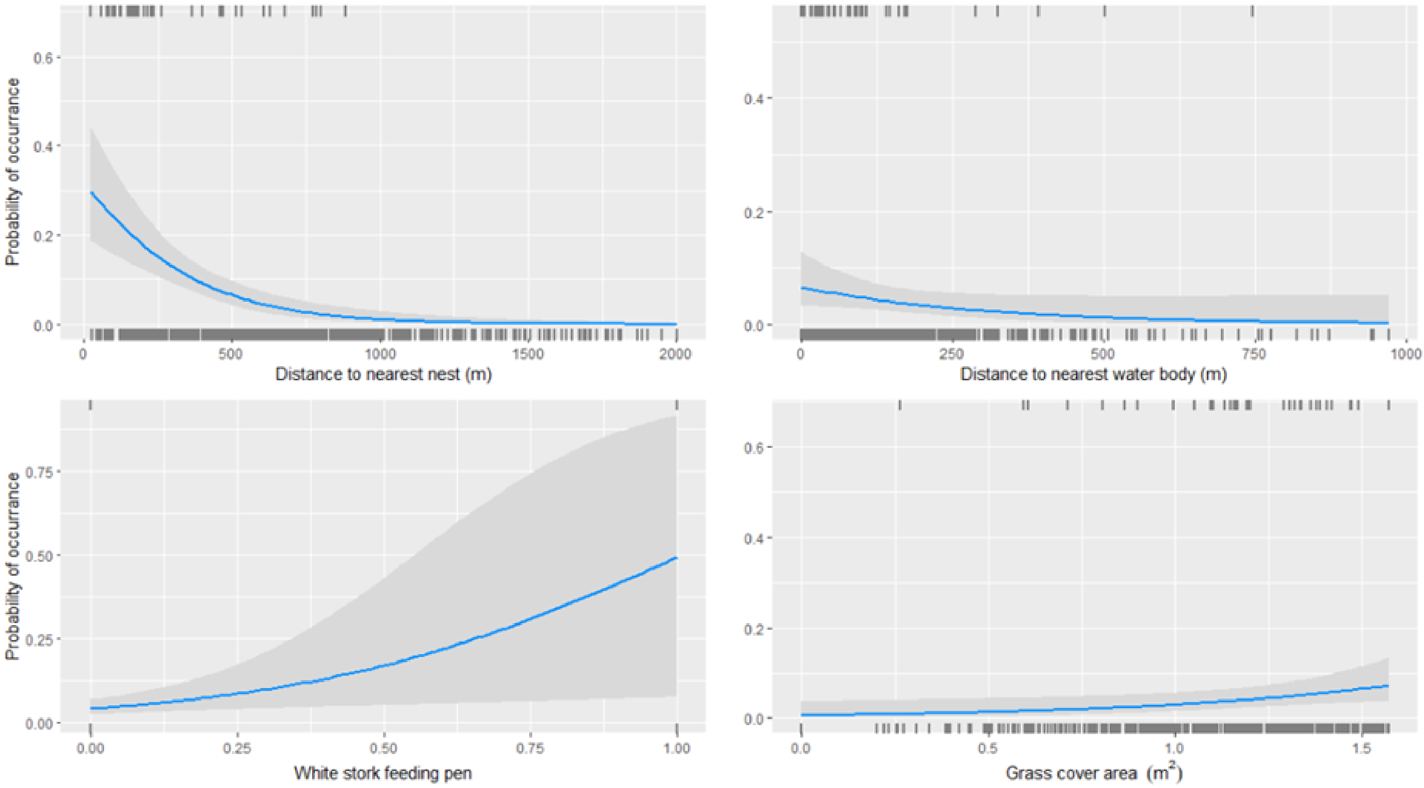

Figure 2: Prediction curves generated from generalised linear models showing the probability of occurrence for white storks in the study area based on different environmental variables at 100 m resolution.

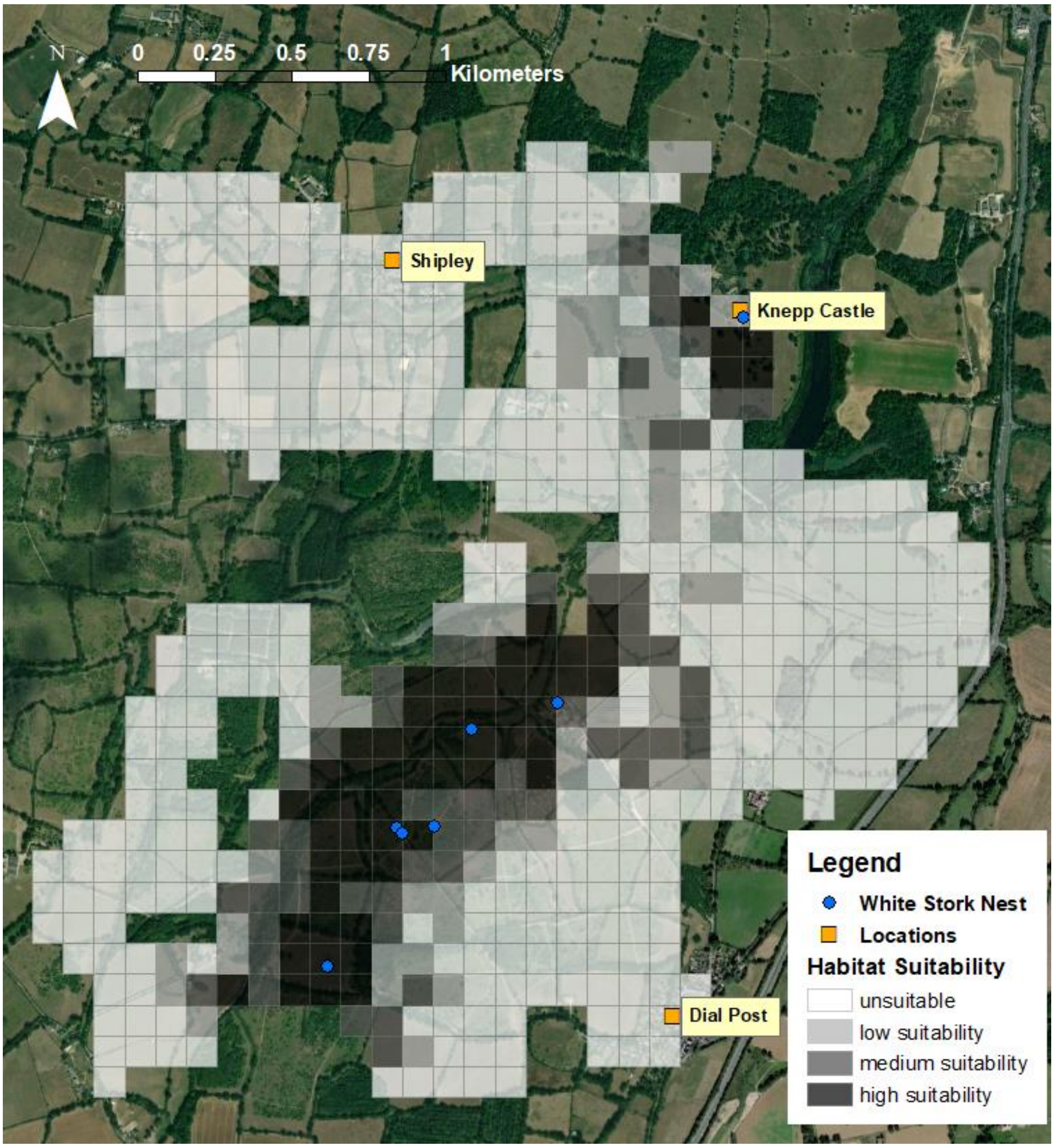

Figure 3: Habitat suitability model and suitability classes for white storks (*Ciconia ciconia*) at the first reintroduction site in the UK.

For the micro-scale analysis (10m), 51 presence points were used to generate 510 pseudo-absence points. The model with the lowest AICc (model P1) contained the variables 'Distance to a nest' and 'Distance to a water' which were both negatively correlated with stork presence. There were 4 further models which were also within ΔAICc≤ 2 of the most reduced model P1. Models P2, P3 and P4 all contained 4 variables: the same three as P1 as well as the variables 'grass height', 'livestock units' and 'disturbance index' respectively. Model P5 contained the same variables as P1 as well as 'grass height' and 'livestock units' (Table 7). Since the variables 'livestock units' and 'disturbance index' both had standard deviations greater than their associated coefficients, meaningful interpretations of these variables could not be made and therefore were not graphically represented.

Table 7: Selection of the five best generalised linear models and their coefficient explaining variation in the probability of white stork presence. Also shows log-likelihood function (logLik), Akaike information criteria with correction for small sample sizes (AICc), AICc differences (Δi) and Akaike weights. SD = standard deviation

Model	Intercept ± SD	Grass Height ± SD	Livestock Units ± SD	Distance to nest ± SD	Disturbance Index ± SD	Distance to water ± SD	logLik	AICc	Δi	Akaike weight
P1	-1.162 ± 0.311			-0.002 ± 0.002		-0.004 ± 0.001	-162.226	330.5	0	0.181
P2	-0.832 ± 0.407	-0.207 ± 0.167		-0.002 ± 0.001		-0.004 ± 0.002	-161.424	330.9	0.43	0.147
P3	-1.033 ± 0.336		-0.338 ± 0.358	-0.002 ± 0.001		-0.005 ± 0.002	-161.733	331.5	1.04	0.108
P4	-0.127 ± 1.235			-0.019 ± 0.001	-0.496 ± 0.572	-0.005 ± 0.002	-161.865	331.8	1.31	0.094
P5	-0.707 ± 0.424	-0.204 ± 0.165	-0.338 ± 0.3588	-0.002 ± 0.001		-0.005 ± 0.002	-160.936	332	1.49	0.086

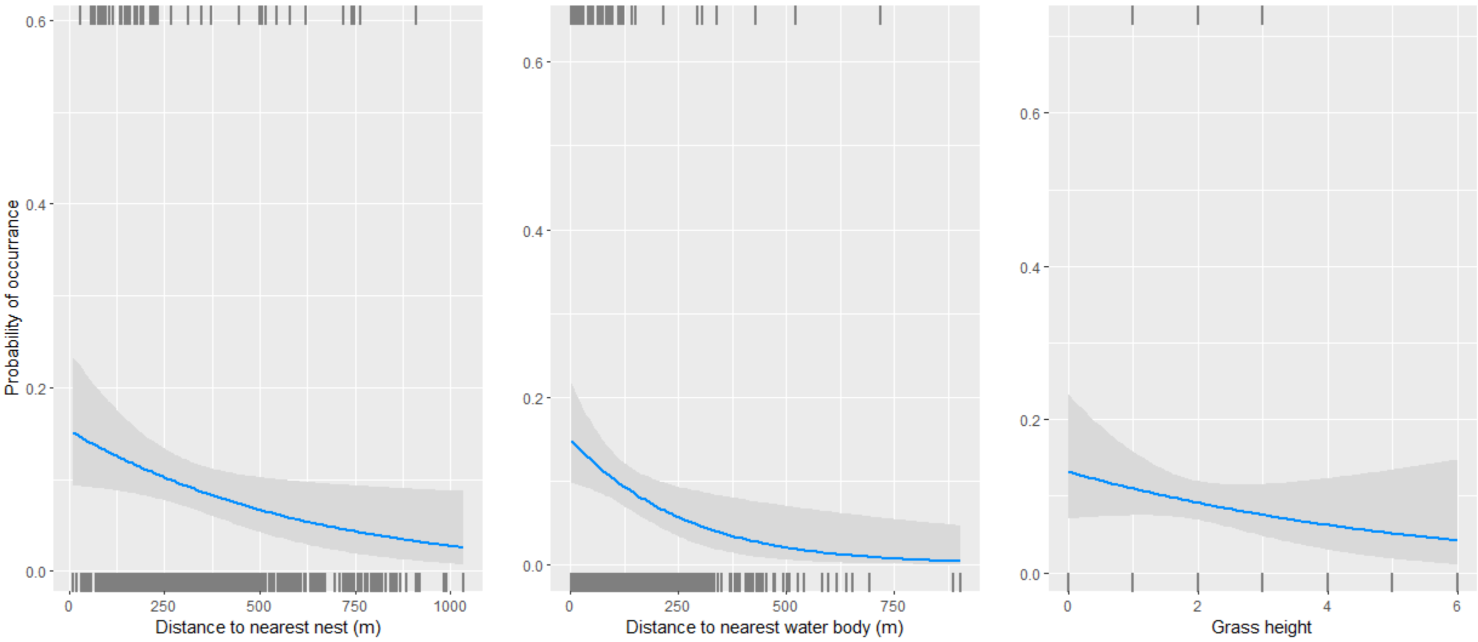

Figure 4: Prediction curves generated from generalised linear models showing the probability of occurrence for white storks in the study area based on different environmental variables at 10m resolution.

3.5 Discussion

This is the first study to examine white stork foraging habitat selection using field data from breeding birds, following the species reintroduction in the UK. Both the local and micro-scale analysis identified similar relationships between the explanatory variables and white stork presence, providing strong evidence that this species selects open habitats with short grass near water where the grass as their preferred foraging habitats. The pen, where injured and flightless birds are kept and fed, was also positively selected by this new population. Furthermore, at both scales, distance to the nearest nest was an important explanatory variable, with white storks more likely to be found foraging near nest locations.

These results coincide with what was found in other areas of the species' distribution radius of 5km around the nest is commonly cited at the maximum foraging extent for white storks (Johst et al., 2001; Zurell et al., 2015) although storks will forage closer to the nest if the habitat is optimal (Alonso et al., 1994). Availability of high-quality habitat in the immediate vicinity of the nest can help breeding storks supply enough food to their chicks (Janiszewski et al., 2013) and is an important factor to consider in reintroduction projects. The study area includes a white stork feeding pen, which was actively selected by the storks due to being high-calorie, low effort source of food (Golawski & Kasprzykowski, 2021; Stephens & Krebs, 2019). Storks are often considered as opportunistic feeders, typically eating what is easily accessible to them (Antczak et al., 2002; Chenchouni, 2017) and have been able to successfully utilize several anthropogenic food sources (Arizaga et al., 2018; Ferreira et al., 2019; Gilbert et al., 2016). Supplementary feeding can significantly improve white stork reproductive success (Hilgartner et al., 2014; Massemin-Challet et al., 2006) and it has been used as a management tool in other white stork reintroductions (Olsson & Rogers, 2009; Schaub et al., 2004) As this population grows the reliance on this supplementary food source should be investigated to better understand its impact on breeding success and potential implications for the reintroduction project.

Distance to water was found to be an important predictor at both the local and micro scale, with the probability of white stork presence increasing with proximity to water. White storks' close association with inshore water in agricultural landscapes has been well documented across Europe (Alonso et al., 1991; Olsson & Rogers, 2009; Wojciechowski & Janiszewski, 2020). In other habitat suitability models based on white stork populations in Sweden and southeast Europe, the wetness of the landscape was shown to be a strong predictor of stork presence (Olsson & Rogers, 2009; Radović et al., 2015). Several studies have also shown that nesting in close proximity to wetter landscapes such as water meadows, river valleys and wetlands is associated with greater reproductive success potentially due to these habitats having greater food availability compared to drier surrounding areas (Janiszewski et al., 2014; Nowakowski, 2003; Tryjanowski et al., 2005).

Vegetation structure is important for UK storks, with white storks preferring to forage in open areas of grassland (‘grass cover’). These findings were consistent with other studies showing that wooded and scrubby habitats are generally avoided by white storks (Carrascal et al., 1993; Zurell et al., 2018), although there have been a few observations of white storks foraging on woodland edges in Poland (Tryjanowski et al., 2018). Furthermore, this study found UK white storks preferred shorter grass heights, but this relationship was influential only at a micro-scale. It is well reported across the literature that white storks prefer shorter grass as it is easier to locate prey and it provides less resistance to movement leading to greater feeding efficiency (Golawski & Kasprzykowski, 2021; Marcin Rachel, 2006; Moritzi et al., 2001). A potential reason why this relationship was not captured at the local level could be due to sample size as this reintroduction is still within the initial stages and the population is small. Alternatively, there could be substantial variation in grass height across large areas of the reintroduction site, due to the free moving livestock and deer within the estate grounds (Knepp Wildland, 2022), resulting in foraging decisions being made at a finer scale.

In grassland habitats large herbivores such as cattle and ponies can be influential ecosystem engineers, reducing sward height and opening up woody or scrubby landscapes landscapes (Nugent et al., 2022; Tälle et al., 2016) Even at low densities, deer can significantly supress woodland regeneration through their consumption of tree saplings (Gill & Morgan, 2010). Furthermore, white storks were found to have greater foraging efficiency in fields which contained cows compared to those without even though the height of grass in both field types were the same (Zbyryt et al. 2020). The increased foraging efficiency could be due insects being attracted to the tracks and dung the cows produced (Zbyryt et al. 2020) or that they were disorientated by the cattle’s movements making them more vulnerable to attack (Dinsmore, 1973; Kosicki et al., 2006). So, whilst the models in this study could not detect a clear relationship between white stork presence and livestock units, their indirect effects on vegetation structure and wider biodiversity could be significant in influencing habitat suitability in the future. For future studies, we would recommend surveying each herbivore species individually using methods that could more accurately capture their movement and grazing behaviour. This would lead to a finer understanding of the different roles these herbivores play in shaping this landscape.

Whilst ecotourism is often cited as socio-economic benefit of reintroduction projects (Auster et al., 2020; Hall, 2019), the associated human disturbance created by recreational visitors can negatively impact the species within the area (Ellenberg et al., 2006; Monti et al., 2018; Müllner et al., 2004). Along the busiest section of footpath surveyed, walkers were encountered at an average rate of 4.5 people/km however there was no relationship found between foraging locations and the disturbance index suggesting the current levels of ecotourism and associated disturbance is not an important factor for foraging habitat selection in the study area. Upon writing there did not appear to be any studies directly measuring the impact of walkers on white storks although they have often been observed foraging in the vicinity of agricultural machinery, traffic and people (Andan, 2012; Golawski & Kasprzykowski, 2021) which suggest that this population is tolerant to the level of disturbance created by recreational walkers in the survey area. Proximity to human settlements can even be a significant predictor of white stork nest presence (Radović et al., 2015), with the species regularly nesting on manmade structures, such as the breeding pair nesting on the Knepp Castle during the survey period (Bialas et al., 2020; Tryjanowski et al., 2009; White Stork Project, 2021b). However, during the survey, white storks appeared to forage closer to footpaths in the early morning and evening when there were less people present. Since birds are known to vary their foraging behaviour temporally to adjust to human disturbance (Fernández-Juricic et al., 2004), studying the white storks foraging choices within a 24-hour cycle may result in useful insights which could support the management of this population within this popular rewilding site.

This study highlighted key habitat variables influencing the foraging decisions of this recently reintroduced population. However, one must be cautious before over extrapolating these findings due to the small size of this novel population and the limited time span in which the fieldwork was conducted. A small sample size can negatively impact a model's ability to accurately estimate habitat suitability as potential outliers carry more weight in analyses that would otherwise be buffered by the presence of more data (Shiroyama et al., 2020; Wisz et al., 2008). Additionally, it was not possible to identify individual storks so there is the risk that some individuals were over represented and a level of pseudo-replication could not be statistically accounted for (Colegrave & Ruxton, 2018).

However, since many of the relationships between habitat variables and foraging decisions align with similar studies within the wider literature with far larger sample sizes (Carrascal et al., 1993; Olsson & Rogers, 2009) we are confident that these models are strong enough to support and contribute to our understanding of this novel population in particular. We recommend that foraging habitat preferences should be further investigated as the population grows since a larger sample size would not only contribute to the development of stronger predictive models but could also reveal relationships that only appear at higher levels of intraspecific competition. In turn this can help identify the suitability of future potential reintroduction sites or areas within the UK that would benefit from habitat restoration efforts as seen in Sweden (Olsson & Rogers, 2009).

'Rewilded' landscapes are by definition very dynamic in their composition, as locations which may have been initially identified as highly suitable may shift in response to changes in climate, vegetation dynamics or reintroductions of other species (Perino et al., 2019). The rate in which white storks return to their previous breeding habitat is positively correlated with the quality of that habitat (Janiszewski et al., 2013) so it is important that attractive nesting sites are provided to improve the reintroduction's chance of success. For example, based on these habitat suitability models, we would recommend any artificial nesting platforms to be located near bodies of water and open grassland with short vegetation (Santopaolo et al., 2013). Through implementing these recommendations, we hope that these models can be further developed to support the reintroduction of this species back to the UK.

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4. Concluding remarks

Whilst rewilding was originally focused on returning large areas of land to a historical ‘wild’ where human presence and influence would be minimal to non-existent, it has since softened to accommodate areas where human exclusion would be neither attainable, sustainable or just. Particularly in the European landscape, there has been a recognition that humans should be considered part of, rather than separate from, nature and hence should be included in future-orientated visions of wilderness where ecological process and biodiversity thrive alongside people. However there remains a paradox between the necessary ‘hands-on’ stance required to ensure a reintroduction’s success when it is heavily associated with the ‘hands-off’ attitude that rewilding promotes. Beyond supporting the species, itself, I hope the return of this charismatic bird will not only improve the recognition and support needed for wetland habitats but also improve attitudes towards the reintroduction of other species within the UK that can also aid in restoring ecosystem function and contribute to reversing the current trends in biodiversity loss.

The thesis cautiously suggests a hopeful outcome for the future of the white stork population within the UK. The population viability analysis conducted in Chapter 1 indicates that if a small proportion of the population overwinters within the UK which current data on dispersal behaviour suggests is likely to occur, then the population should persist in the long-term. If this is not the case, the population will likely respond positively to realistic management actions to promote a positive growth rate. Within Chapter 2, the white stork population indicated similar foraging behaviour and habitat preferences as other reintroduced and naturally occurring white stork populations across Europe suggesting that the Knepp Castle Estate currently provides suitable reintroduction habitat.

Whilst I believe these chapters have provided value at this early stage of the white stork’s reintroduction, many of the weaknesses within this thesis stem from a limited amount of demographic and behavioural data and by only having access to a small sample size due to the infancy of the population. As the project continues, trends in dispersal and migratory behaviour will become clearer which will also impact the genetic diversity of the population. It would be advisable to incorporate such data into future population viability analyses to increase the model’s utility. Additionally, I recommend continued monitoring of the white stork’s foraging behaviour as well as the habitat composition of the Knepp Castle Estate and surrounding areas as the combination of large, free-moving herbivores coupled with the recent reintroduction of Eurasian beavers (*Castor castor*) which occurred after the survey period has created a highly dynamic landscape that will continue shifting composition over the coming years. Additionally, the impacts of climate change are likely to not only influence which areas are attractive to the storks at Knepp, but the proportion which choose to overwinter within the UK. By studying this population closely, we will improve our ability at assessing the reintroduction’s progress, responding to any difficulties if they arrive and ultimately deciding when human management is no longer needed to sustain the population and marking the reintroduction as a success.