Using population modelling to understand the dynamics of the Sussex peregrine falcon (*Falco peregrinus)* population

by

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List of Abbreviations

UK	United Kingdom
USA	United States of America
PVA	Population Viability Analysis
GIS	Geographic Information Systems
r	The mean population growth rate
SDI	Standard deviation of the stochastic population growth.
SPS	Sussex Peregrine Study
IUCN	International Union for the Conservation of Nature
WW2	World War 2
DDT	Dichlorodiphenyltrichloroethane
K	Carrying Capacity

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Abstract

The peregrine falcon, *Falco peregrinus*, is a charismatic bird of prey, which belongs to the Family Falconidae. It was once listed as an endangered species, but through dedicated conservation efforts it is now of least concern. The peregrine falcon is the perfect case study for measuring the impact of conservation efforts on species on the brink of extinction, with just 360 pairs remaining in 1963, which have since recovered to 1750 thanks to the conservation efforts taken. The focus of this study was on the peregrine falcon population of Sussex, in which the data was provided by the Sussex Peregrine Study (SPS) who have one of the most comprehensive historical records of peregrine falcons. Using the data provided, Geographical Information Systems (GIS) and Population Viability Analysis (PVA), many different population elements were analysed in a historical context, such as the density and location of peregrines, the productivity of the population and the probability of survival of populations at different time points. Using the more recent records, the recolonising population was explored and compared to the historical records. As this population is a new inhabitance of the county of Sussex, the peregrines nesting preferences were also analysed, indicating factor preferences such as location and nest type. As the modern population has exceeded historical records, nests have been established further north than previously witnessed. Records show a pattern of high egg and young productivity in the early 1900s (and before World War 2) and 1990-2016, with 1941-1988 having minimal productivity, showing the direct relationship between the successful production of young, the stability of a population and anthropogenic pressures. The early low productivity and relatively small number of birds in the early 1900s were caused by egg collection and persecution, while the later lack of productivity and final disappearance of peregrine falcons were due to organochlorine pesticide poisoning. From the different nest types being established, an order of preference has been established which is coastal, inland and manufactured from most to least favoured. An analysis of the records indicate that this is also the order of most to least productive nest type. The PVA based on current (optimal) parameters indicated that the stable pre-crash population could have continued to grow under these conditions; however, the 1941 population was already too diminished to survive even in the optimal conditions. The 0-productivity simulation indicated that all populations would go extinct, as no offspring would be created to continue the population. The persecution model indicated that more robust stable populations could survive these conditions; however, persecution had a greater effect than lack of productivity on smaller populations. The model which mimics the conditions witnessed in the population crash of the peregrine falcon shows that no population, no matter how robust, would survive under these circumstances. In conclusion, the indirect conservation efforts taken in the UK to protect the peregrine falcon population were incredibly successful as they tackled the primary issue of productivity, while reducing the lesser impact of persecution which is detrimental for smaller populations. Lessons can be learnt from this study and applied to other raptors facing population declines or slow recovery rates.

Keywords: Birds of Prey, Conservation Biology, Peregrines, Population Biology, Population Viability Analysis, Raptors.

Introduction

The peregrine falcon (*Falco peregrinus*) is a charismatic bird of prey of global distribution, found in all continents except Antarctica, and consisting of 19 subspecies (Hoyo, Elliott and Sargatal, 2003). Although it is considered as a Least Concern species for conservation by the International Union for the Conservation of Nature (IUCN, 2021), it is admired by different cultures for its speed, agility and hunting behaviour, and has also been in the front line of conservation efforts due to population declines (Bell et al., 2014).

Peregrine falcon populations have been severely affected by persecution, environmental pollution, trade and habitat degradation, mostly during the second half of the 20th century (Ratcliffe, 1980). This have led to significant population declines and extirpations (local extinctions) in many countries and became endangered in the 1950s, 60s and 70s (Nygård et al., 2019; Saar, 1985; Sielicki and Sielicki, 2015). Global and country-specific conservation work and changes to legislation helped peregrine falcon populations to recover (Crick and Ratcliffe, 1995; Dzialak Lacki and Vorisek, 2007; Fletcher et al., 1999; Levain et al., 2015). Notably, there are examples of successful conservation efforts through reintroduction programmes in Canada, United States of America (USA), southern Scandinavia, Germany and Poland, showing that peregrine falcon populations can be reintroduced after suffering localised extinctions (Holroyd and Bird, 2012; Lifjeld et al., 2002; Saar, 1985; Sielicki et al., 2009; Watts et al., 2018). In southern England, however, there were never formal reintroduction programmes for peregrine falcons, and particularly in Sussex they made a surprising come-back from a local extinction in the early 1990s after having disappeared for more than 30 years (Franklin and Everitt, 2009; Weaving et al., 2021).

In this thesis, the population of peregrine falcons in Sussex is studied trying to answer the questions: What is the distribution, size and productivity of the current peregrine falcon population in Sussex? What is the population structure and dynamics of peregrine falcons in the Sussex coast, and specifically comparing before and after the mid-20th century population crash? What is the chronology, rate and direction of recolonisation in coastal, inland and manufactured sites? This is studied using a unique data set on peregrine falcons collected since the early 1900s to date, and combining the data with population modelling software and Geographical Information Systems (GIS).

Peregrine Falcons as Raptors

Raptors, also known as birds of prey, is a term used to describe birds that actively hunt and feed on animal flesh, specifically mammals, reptiles and other birds, and are distinguished by having a hooked bill for tearing off flesh, keen eyesight for detecting their prey from long distances or at night, and sharp talons for grasping and killing prey. Raptors make up the four taxonomic orders: Accipitriformes, Falconiformes, Cariamiformes and Strigiformes (Stevenson, 2010; Taylor, 2010). Raptors are ecologically important as apex predators and are considered as ideal indicator species and keystone species for conservation purposes (Bildstein, 2001). As apex predators, it can be assumed that a larger population size of raptors will indicate a healthier population of their prey species, as a larger number of prey will be able to sustain a larger predator population (Hewitt, 2011). Similarly, if the prey population is lower in size, the predator population can be expected to follow a similar trend (Schaller and Keane, 2009). Pesticide poisoning, disease or persecution can affect these natural predator-prey trends, indicating that human impacts are impacting natural populations (Stevens, 2010).

The peregrine falcon is a large member of the order Falconiformes at approximately 34-58 centimetres of body length and wingspan of 74 to 120 cm, but can vary greatly among subspecies (Cade et al., 1988). The peregrine falcon also possesses sexual dimorphism in mature individuals, with females being much larger (700-1500 g) than males (330-1000 g) (Snow, 1998). The peregrine falcon is known to migrate in many regions (Bell et al., 2014), which is the reason of its common and scientific name ('peregrinus' – to wander or to travel from place to place, or to peregrinate). Throughout the regions in which the peregrine falcon can be found, there are 19 known subspecies showing many morphological differences, ranging from different colours, different breast marking density and shape, different facial markings, different sizes and different weights (Ellis et al., 2020; Zuberogoitia et al., 2009). Examples of this would be *F. p. pealei*, which is the largest subspecies, of darker colouration and possessing a very wide bill, and *F. p. babylonicus* , which is one of the smaller subspecies and of paler colouration (Snow, 1998; White et al., 2002).

The peregrine falcons found in the UK are of the subspecies *F. p. peregrinus*, with the males averaging between 580-750 g, while the females average 925-1300 g (Snow, 1998). The majority of peregrine falcons found in the UK do not migrate; however, some individuals from Scandinavia will migrate to Britain over winter (Ratcliffe, 1984). In the UK, the peregrines usually lay their eggs between March and April which take up to 32 days to incubate and then hatch (Mearns, 1983). The oldest recorded peregrine falcon in the UK lived to 21 years 10 months, while the average lifespan is much lower at 7 years (Robinson, 2005). The peregrine falcons in the UK have been documented nesting in various locations, including coastal cliffs, inland quarries and manufactured structures such as skyscrapers, nest boxes or electricity pylons (Sussex Peregrine Study, n.d.).

Peregrine Falcon Declines

Raptor populations have previously suffered great declines, globally, due to pesticide poisoning and persecution (Madden, Rozhon and Dwyer, 2019; Porter and Wiemeyer, 1969). As apex predators, raptors are highly susceptible to bioaccumulation, a process in which contaminants in the environment work their way through the organisms in the food chain (Franke et al., 1994). Due to the nature of energy flow and trophic levels, just a fraction of the energy passes from one trophic level to the next (Hairston and Hairston, 1993). This leads to the apex predator having to consume a much higher quantity of food to acquire an equal amount of energy compared to the producers (Pimm and Lawton, 1977). Due to this level of food consumption, any contaminants found in the prey will be passed upwards across trophic levels, causing large quantities to be present in the apex predator, which in many cases will cause adverse effects such as death, fatigue and reduced breeding fitness (Cooper et al., 2017; Johnson, Lepak and Wolff, 2015).

After World War 2 (WW2), the adoption of organochlorine pesticides increased rapidly with its usage being witnessed in all continents except Antarctica. This led to many habitats becoming contaminated with the various organochlorine pesticides, such as Dichlorodiphenyltrichloroethane (DDT), dieldrin and aldrin (Hoyo, Elliot and Sargatal, 2003; Kaushik and Kaushik, 2007). The widespread adoption of organochlorine pesticides ultimately led to the death of a large portion of raptor populations through bioaccumulation (Thirgood, Redpath, Newton and Hudson, 2000; U.S. Fish & Wildlife Service, 2021). A specific example of this was the poisoning of bald eagles (*Haliaeetus leucocephalus*) in North America through the use of DDT (Grier, 1982). During the period of heavy usage of pesticides following WW2, the bald eagle population was documented to be as little as 417 nesting pairs, but since the implementation of an organochlorine pesticide ban in 1972, which included DDT, plus other conservation efforts, the population recovered and it has now surpassed 300,000 individuals (Bowerman et al., 1995; U.S Fish and Wildlife Service, 2020).

Another issue many raptor populations are facing in many countries is persecution. As a predator, people may feel threatened by the presence of birds of prey or may see them as competition to their hunting, and raptors could be perceived as hunting trophies. Raptor persecution became common after the emergence of firearms, which enabled hunters to kill their prey more easily and without the need to host a domestic raptor as a companion (RSPB, n.d.). (Here, the term 'domestic' is used to describe a wild animal, or an animal descendant of wild-take, that is raised by humans, but not a domesticated animal, which is the results of a process that involves selective breeding and artificial selection.) Raptors are often seen as competition for the hunters' game, and the advent of reliable firearms used for hunting also brought around the hobby of sport shooting which led to the creation of grouse moors managed by game keepers, from which raptors had to be eliminated from (Thirgood et al., 2000). The gamekeeper's priority was ensuring the game kept on their land was alive and healthy, leading to the extermination of raptors found on their land (Newton, 2020). One of the methods used to remove the raptors from the land was using poisoned bait traps; however, this method was indiscriminate and would also kill raptors that posed no risk to the gamebirds, such as the honey buzzard or short-eared owl (Garmyn et al., 2021). The fear and competition posed by the raptors lead to huge numbers being shot and intentionally poisoned to remove them from the areas (Bortolotti, 1984). The main groups conducting these persecutions include farmers, gamekeepers and hunters. As education on raptors improved and legislation has been introduced, raptor persecution in many countries has decreased; however, many illegal killings still occur (LeFranc and Millsap, 2006).

In the UK there are 15 species of raptor, five of which were driven to extinction before 1914 and another five declining to fewer than 100 breeding pairs between 1870-1970 (Holden and Gregory, 2021; RSPB, n.d.; Taylor, 2010). The five raptors that went extinct in the UK include the marsh harrier (*Circus aeruginosus*), white-tailed eagle (*Haliaeetus albicilla*), honey buzzard (*Pernis apivorus*), goshawk (*Accipiter gentilis)* and osprey (*Pandion haliaetus*) and the five raptors that saw rapid declines were the hen harrier (*Circus cyaneus*), hobby (*Falco Subbuteo)*, golden eagle (*Aquila chrysaetos*), red kite (*Milvus milvus*) and Montagu's harrier (*Circus pygargus*). As with birds of prey from other regions, the primary drivers of population declines and local extinctions were persecution and pesticide poisoning. Shooting for sport became very widespread in the 19th century ramping up raptor persecution greatly, thus resulting in population declines (McMillan, 2011). The increased rarity of these persecuted birds then made their eggs and skins more desirable to collectors, further decimating the population due to egg collecting and trophy hunting (Ratcliffe, 1963). Bird enthusiasts and ornithologists have known that egg collecting alone created a period in which the productivity of Sussex was close to zero, as all the eggs were being taken, so no young could be produced (Sussex Peregrine Study, n.d.). It must be noted that, egg productivity in this study is used to refer to the average number of eggs laid – and hatched – per active nesting site. Egg productivity in this context is different from the biological concept of 'productivity' which is used to indicate the number of eggs laid per active nesting site, not taking into account the success of the eggs laid.

The peregrine falcon was dramatically affected in the UK, the USA and Canada, and in other developed regions of the world, as it was not only subject to persecution but was also extremely susceptible to organochlorine pesticides (Brown, 1997). During WW2, persecution of peregrine falcons increased when the UK government ordered the culling of these birds to protect their carrier pigeons (Dennis, 2022). Post WW2, pesticide use caused eggshell thinning, decreased successful mating, and increased mortality in adults and chicks (Brown et al., 2007). With these main factors acting together, the peregrine falcons saw a drastic decline in their population, with just 360 pairs remaining in the UK in 1963 (Ratcliffe, 1993). In contrast to this, a survey of the recovered population, conducted in 2002, estimated a population of 1,402 breeding pairs (Robinson, 2005). However, this new population was only attainable through drastic conservation measures put in place in the UK to conserve the biodiversity of the time. It must be noted that the measures that successfully prevented the complete extinction of the peregrine falcon in the UK were not introduced specifically for this species, but instead they were put in place to protect a wide array of different species through the Wildlife and Countryside Act of 1981 and the restriction of organochlorine pesticide use (Brega, 2022; Wildlife and Countryside Act, 1981).

The peregrine falcon also suffered from egg collectors, who raid the active nesting sites of peregrine falcons to add eggs to their collection, which affected the reproductive success and recruitment of new birds into the population (Ratcliffe, 1980). Peregrine falcon eggs are considered particularly interesting to egg collectors as every egg has a unique pattern of red swirls and blotches seen on no other (Taylor, 2010). Some nests are also raided for the acquisition of viable peregrine falcon eggs to be incubated and hatched for use in falconry (London Peregrine Partnership, 2022). Although many captive-bred peregrine falcons are available, some falconers desire wild-bred birds which results in legal or illegal wild-take further impacting the wild populations. When in combination with persecution and poisoning, these factors led to the near complete collapse of British peregrine falcons in the 1950s (White et al., 1980).

When considering suitable methods to successfully conserve the UK population of peregrine falcons, persecution and pesticide poisoning are the main factors that were directly tackled. The number of peregrine falcons being killed was greatly reduced through the introduction of many legislations protecting them such as the Wildlife and Countryside Act of 1981 (Wildlife and Countryside Act, 1981). This act had three main points concerning wild birds: it was made illegal to kill or injure a wild bird, alongside making it a criminal offense to take, damage or destroy active nests, and taking or destroying the eggs of a wild bird was also made illegal (Wildlife and Countryside Act, 1981). The peregrine is also a Schedule 1 species under this act, meaning the punishments for committing an offence against this species are the most severe.

When tackling the organochlorine pesticide poisoning issue facing the UK ecosystems, there were two progressive steps taken. The first one was a voluntary reduction in organochlorine pesticide usage conducted over multiple phases which began in 1962 (RSPB, 2022). This assisted in reducing the damage caused by the pesticides; however, as it was voluntary, organochlorines were still widely used as a pesticide. In 1982 this was then followed by an almost complete ban of DDT, aldrin, dieldrin and endrin (Fletcher et al., 1999; Levain et al., 2015).

Global Peregrine Falcon Population Recovery

In response to the peregrine falcon collapse witnessed globally, there were two main approaches used in the conservation of the species: indirect and direct support of the populations. Indirect measures focused on the factors causing the collapse through laws preventing the persecution of the falcon, laws prohibiting the collection of egg of the species, or critically, the banning of organochlorine pesticides which was causing the drop in peregrine falcon productivity. Direct support would be through the addition of captive bred individuals to a population, which while preventing the local extinction of a population, could not prevent the continued decline of the species on a larger scale. In the conservation efforts observed in the 20th and early 21st century, both approaches were seen being used simultaneously to minimise the loss of adult birds, to maximise the number of young produced and to bolster the wild populations. Examples of countries that successfully employed both strategies include Poland, Germany, Sweden, Norway, Denmark, USA and Canada. The UK provides a rare example of a country in which only indirect measures were taken. Despite the fact that no direct measures were taking to support the UK peregrine falcon population, a significant increase in peregrine falcons and productivity were witnessed. This observation allows further insight into the recolonisation of a collapsing species population, as it documents the history and growth of a species, under conditions not well documented globally.

The USA and Canada, who had a successful conservation strategy for peregrine falcons, used both direct and indirect conservation measures to support their collapsing populations. While both territories enforced measures such as the banning of DDT, the protection of nesting birds and their habitat, the North American territories also put a strong focus on the release of captive reared birds (Crick and Ratcliffe, 1995; Dzialak, Lacki and Vorisek, 2007). Prior to the population crash, peregrine falcons were found over the entirety of North America, with an approximate population of 3,875 breeding pairs in the 1940s (Fish and Wildlife Service, 1999). By the height of the global population collapse, the eastern populations of USA peregrines went extinct and the western populations had declined to around 90% of their pre-crash population, with only 324 recorded nesting pairs in 1975 (Hoffman, 1999). The USA banned the use of DDT in 1972, which would have eliminated a large number of mortalities caused due to eggshell thinning (Jaga and Dharmani, 2003). The USA additionally bolstered their populations through the release of captive born birds which underwent ‘hacking’, a process in which the falcons were reared in partial captivity to ensure they could survive alone, while not becoming dependant on humans, only being released once they could adequately hunt for their survival (Dzialak et al., 2006). The initial releases were conducted in 1974, with 6,221 birds being released in total by the end of the program (Enderson et al., 1995). Due to the conservation strategies put in place across North America, the peregrine falcon population is now estimated at approximately 3000 breeding pairs and can be found within all their previous territories (Cade et al.,1997; NPS.gov, 2021). The success of the conservation efforts led to the removal of peregrine falcons from the US Endangered and Threatened Species list in 1999 (French, 2023).

Poland saw a suspected complete extinction of their peregrine falcon population, with no recorded nests within the country in 1964 (Sielicki and Sielicki, 2015). In response to this, various indirect and direct conservation efforts were put in place. In 1976, Poland banned the use of DDT in an effort to increase the productivity of their breeding raptor populations (Malusá et al., 2020). Additionally, Poland introduced The Polish Act on Nature Conservation in 2004, which prohibits the capturing, killing or disturbance of peregrine falcons and their nests (Kuchciński, 2004). In 1990, Polish falconry groups led the reintroduction efforts of the species, with a focus primarily on the forest-nesting populations (Sielicki and Sielicki, 2007). The birds were raised in a method similar to the North American 'hacking' in which they could not interact with humans when being fed, to avoid a dependency of humans from the reared individuals (Gajda, 2012). From the period of 1990-2009, 350 peregrine falcons were released into Poland (Puchała et al., 2022). The release of peregrine falcons in Poland has been a continuous process with additional birds being released each year since 1990, with the reintroduction program being overtaken by the Falcon Wildlife Association in 2010 (Falcon Wildlife Association, n.d).

Between 1950-1960 a population of no greater than 50 pairs were recorded in Germany, with no populations north of the Main River (Saar, 1985). In 1973 peregrine falcons were reported as extinct in eastern Germany, which at the time was the German Democratic Republic (Kleinstäuber, Kirmse and Langgemach, 2018). To counteract the declining populations of peregrine falcons in Germany, the Federal Nature Conservation Act was created, and DDT was banned in both east and west Germany. The Federal Conservation Act prohibits the destruction, damage or disturbance of bird nests of endangered species in any way which could impact the breeding or rearing of the individuals (Federal Nature Conservation Act, 2021). Furthermore, this act prohibits the capture, pursuit, killing, injuring or disturbance of protected species and breeding European birds. As Germany was split into two political entities during the period of the organochlorine use, there are varying dates in the implementation of a ban on DDT. West Germany banned the usage of DDT in 1972, while it was not until 1988 that East Germany banned the use of organochlorine pesticides (Aichner et al., 2013). In 1974, Germany was successful in breeding their first captive bred peregrine falcons, which three years later, in 1977, were used in a captive release program (Speer, 1985). The birds were released using the 'hacking' method to maximise their chance of survival once released. From the initial release in 1977 up until 1985, 101 individuals were released with many surviving and producing wild offspring, alongside a high uptake in previously established historic nests (Saar, 1985). The captive rearing project has continued since the initial releases, with 55% of tree-fledged peregrines coming from captive breeding in 2009 (Kleinstäuber et al., 2018).

All Scandinavian nations suffered huge peregrine population losses during the time of organochlorine pesticides use; with Sweden losing 98.3% of its population with a minimum of 900 pairs in the 1920s to 15 pairs in 1975, Norway suffering a loss of 98.4% of its breeding pairs with a reduction from 500 estimated pairs prior to the crash to 8 breeding pairs after and during the population crash, and Denmark saw its final breeding attempt in 1972, with no further successful attempts until 2001 (Andreasen et al., 2018; Nygård et al., 2019; Sielicki and Mizera, 2008). In response to the collapse of the Scandinavian populations, each country implemented measures such as the banning of DDT, the protection of the species and the release of captive reared individuals. Each country introduced bans and restrictions on the use of DDT, with Sweden and Denmark introducing the laws in 1970, and Denmark implementing the ban in 1969 (Conway et al., 1969; Dahllof et al., 2009; Sielicki and Mizera, 2008). In 2008, Norway introduced The Nature Diversity Act, which protects all birds and their nests from unnecessary harm or suffering (MoCE, 2008). This legislation further extends to protect genetic diversity through the non-disturbance of feeding or roosting areas and migratory routes. Sweden created the Species Protection Regulation in 1998, which protects all species of bird, outlawing their capture, killing, disturbance or trade (Miljödepartementet, 1998). Denmark created the Nature Conservation Act and, The Order on the Protection of Certain Animal and

Plant Species and The Care of Injured Game in 1992 and 2021, respectively (MoE, 1992; MoE, 1993). These acts protect all listed birds from killing, capture, trade, egg collection, nests disturbance and nest destruction. Scandinavian countries also undertook direct conservation measures through the implementation of captive rearing and release programs to bolster the populations (Jacobsen et al., 2007). The reintroduction process was undertaken in 1974 using birds of Scandinavian, Scottish and Finnish origin, to maximise genetic diversity in the prospective populations, thus minimising the risk of genetic bottlenecks due to genetic homogeneity (Lindberg, 2007; Nesje et al., 2000). The captive-reared birds were raised in a 'hacking' method, similarly to the North American subjects to increase their chances of survival in the wild. From the initiation of the project up until 2007, 439 young survived fledging and were released into the wild in Sweden (Lindberg & Sjoberg, 2009; Lindberg & Nesje, 2015). In 2007 Sweden had between 150-175 breeding pairs, possibly due to the conservation efforts put in place, presenting an increase of 1000% from 1975 (Lindberg, 2007). Denmark recorded 24 breeding pairs in 2018, an increase of 400% from the estimated 6 breeding pairs prior to the population crash (Andreasen, Falk and Moller, 2018). Prior to the population crash Norway had an estimated number of 500-1000 breeding pairs, but by 2013 this estimation had reached 700-1000 breeding pairs, indicating the effectiveness of conservation measures, allowing the population to exceed the pre-crash values (Nygård et al., 2019). All Scandinavian countries have seen a growth in peregrine falcon population through the implementation of conservation measures, indicating the efficacy of the measures put in place and their importance for the survival and growth of the peregrine falcon population.

While the release of captive reared birds assisted in bolstering the populations, it has been determined that the main cause of the population collapse is due to the lack of productivity due to the effects of organochlorine pesticides (Armstrong and Ratcliff, 2010; Nygård, Sandercock, Reinsborg, and Einvik, 2019). Due to this factor, it can be expected that the banning of DDT was the primary cause of the population recoveries seen in Europe and North America; however, the captive-rearing programs would have likely increased the speed of recovery of the populations through the direct increase of local populations, allowing more individuals to reach maturity and produce offspring.

Peregrine Falcons of Great Britain

Prior to the global peregrine population crash due to the use of organochlorines, the species could be found widespread in all the countries of Great Britain (Robinson, 2005). When examining the various populations of each country, it is known that Scotland has historically served as a stronghold for the species, with England providing the next highest number of breeding pairs, and finally Wales offering potential for breeding pairs of peregrine falcons (Ratcliffe, 1993). Between 1930-1939, Scotland provided nesting habitat for 502 recorded pairs of breeding peregrine falcons, making up 62.7% of the great British population (Ratcliffe, 1980). England hosted 172 peregrine falcon pairs, 21.5% of the population, between the years of 1930-1939 (Ratcliffe, 1984). Wales had 127 recorded pairs of peregrine falcons present between 1930-1939, making up 15.9% of the Great British Population (Ratcliffe, 1980).

In 1961, when the peregrine falcon population crash was underway, the population was surveyed, providing insight into which populations were greatest affected due to the compounding factors leading to the decreasing population. All countries of Great Britian saw a decline in their number of breeding pairs from that recorded between 1930-1939 to that recorded in 1961, with Scotland's population percentage decreasing by 12.4% from 502 to 440 breeding pairs, England's decreasing by 64.0% from 172 to 62 breeding pairs, and Wales's decreasing by 66.9% (Ratcliffe, 1980). These population changes suggest that the Scottish population was the least affected by the factors causing the population collapse, while England was significantly affected, and Wales was the most affected (Ratcliffe 1972). The recolonised peregrine falcon population of Sussex has been found to have a genetically similar makeup to that of the pre-crash population of the United Kingdom, leading to speculation that these population strongholds could have been key contributors to the modern Sussex population; however, further genetic sampling of peregrines from Great Britain, Ireland and continental Europe is required to determine the actual origins of the population (Weaving et al., 2021).

In the South of England, in which this study is focused, dramatic declines averaging 73.7% were witnessed between 1930-1961 (Ratcliffe, 1980). Southwest England saw a decrease from 91 breeding pairs in 1930-1939 to 20 breeding pairs by 1961, a decline of 78.1%. Southeast England saw a decrease from 23 breeding pairs in 1930-1939 to 7 breeding pairs in 1961, marking a decline of 69.6% (Ratcliffe, 1984). Due to the decrease in the peregrine populations in the south of England, it is unlikely that immigration into Sussex would have taken place during this period, or if it were, it would have likely been from outside the expected dispersal range of peregrines.

The Sussex Peregrines Falcons

All the historical records used within this study were provided by the SPS who are a "small group of dedicated enthusiasts monitoring the peregrine population in Sussex since the late 1980's" (SPS, http://www.sussexperegrines.co.uk/). The group was founded in 1990 by Bart Artfield, who on discovering a successful nesting site, after the organochlorine catastrophe, decided it would be incredibly valuable to document the Peregrines recolonisation of Sussex. Through the work of the members of the SPS, they have been able to create one of the most comprehensive records of the peregrine falcon to date, whose work directly provided all the peregrine falcon data from 1990 to 2016, and with continuous efforts to present day. The data collected by the SPS, is provided by a dedicated group of ornithologists, researchers and field surveyors, a full list of members can be found at http://www.sussexperegrines.co.uk/who-we-are.html. The Sussex Peregrine Study ensure a high quality, consistent data set through the use of a standardised data spreadsheet, in which location, total eggs laid, eggs per pair, known young produced, known young per pair, occupation by an individual or pair and type of nest are all documented. This data is collected at a minimum of once annually to ensure the consistency of the data set is upheld. As well as creating their own records for the recolonisation, the SPS have also acquired the diaries of a naturalist and avid egg collector John Walpole-Bond. This discovery provided the SPS with data on all the known Sussex peregrine falcon nests from 1904-1954, covering information such as nest location, year of nest establishment, nest type, nest usage, number of eggs produced each year, number of young produced each year and egg collection. Walpole-Bond's detailed books and records also provided an insight into the Sussex peregrine population of the past, allowing us to know that the population at the time only resided upon coastal cliffs within Sussex leaving the manufactured and inland sights unexplored.

Thanks to John Walpole-Bond and the SPS, the history of peregrine falcons in Sussex is well-documented. In 1912 the peregrine falcon population of Sussex consisted of 24 mature peregrine falcons, with 23 young being produced that year, which was the largest peregrine population recorded in the region prior to the population crash in the mid-20th century (Sussex Peregrine Study, n.d.). Although peregrine falcons were shot and persecuted during WW2, the fatalities had no persisting effect on the local Sussex population and the number of breeding pairs recorded after the war between 1945 and 1951 are comparable to those when records began. However, the population began to show a decline, and subsequent population crash, due to the initial use of organochlorine pesticides linked with indirect mortality of adult birds and eggshell thinning, as well as continuing persecution (Ratcliffe, 1980; Weaving et al., 2021). By 1953, there were no occupied nests and no young produced in Sussex, and the peregrine falcon remained absent from the region as a breeding species for 31 years until 1989 when two mature peregrine falcons were observed and produced a young in 1990. The period until the last breeding pair was observed is called the pre-crash population, while the population studied since the first breeding pair was observed is called the post-crash population. The Sussex post-crash population can then be seen continually increasing and by 1997 the pre-crash peregrine falcon breeding pair numbers were matched. The population continued to increase and by 2016 it consisted of 70 mature peregrine falcons and 50 young. It is therefore of interest to study the reasons behind the natural recovery of the Sussex population, the past and current population trends and dynamics, its chronology, and apparent expansion into what was formerly considered unsuitable habitats.

In recent years, the SPS have maintained their record keeping and further expanding upon it by ringing many of the young produced in the recolonised population. Through the ringing of the young, the age of birds and hatching location can be determined. This can allow further studies to be conducted on the population, such as the dispersion of adult peregrine falcons and their breeding behaviour, such as age of first offspring, and the longevity of birds if the rings can be recovered. The SPS have also assisted in many research projects, covering topics such as conservation genetics and population trends. Through examining the biology of populations of the Sussex peregrine falcon, it may be possible to explain why the peregrine falcons in Sussex have not reached a point of high genetic bottlenecking, despite the native UK population reaching such low population size (Weaving et al., 2021). Through the study of the post pesticide population trends, the pattern of Sussex recolonisation and its rate of expansion may be understood, and this may provide a broader insight into peregrine falcon behaviour, such as nest selection, and may also allow a direct comparison of population trends under different conditions (Franklin and Everitt, 2009).

The peregrine falcon is a prime example of successful conservation efforts through captive breeding and release programmes. But at least in the UK, it is also an example of natural re-colonisation processes that need to be documented and studied to get a better understanding of the factors causing the initial collapse and later recovery of a species (Watson, 1991). For the Sussex peregrine falcon population, the availability of detailed historical and modern-day records provides a unique opportunity to study a pre- and post-crash population to better understand the dynamics of populations affected by anthropogenic activities and discern the main traits of the population and the factors that may represent threats to their natural recovery. When examining the efficacy of the conservation efforts put in place in the United Kingdom, a large increasing trend can be witnessed from the years of 1991-2001, with all countries achieving an 85% or greater increase (Banks et al., 2010). The percentage increase seen in each country were 85%, 91%, 110% and 165% from Northern Ireland, Scotland, Wales and England, respectively (Banks et al., 2010). A similar pattern was also witnessed in the decline of the UK population in 1962 with an average of 80%, 76% and 34% for Wales, England and Scotland, respectively (Northern Ireland was excluded from this study) (Ratcliffe, 1963). When focusing on England, the most significant increase in population percent increase is witnessed in southeast England with an average increase of 445%, while the southwest, the northwest and the west Midlands all had percent increases of 150% or less (Banks et al., 2010).

Many aspects of a population can be studied and learnt using good species records and detailed species biology information coupled with population modelling and GIS. This has been used in this study to estimate population density and generate heat maps showing preferential habitats and breeding areas, to generate maps of the past and present distribution of the nest sites, to show the year-by-year population trends, annual average productivity and population size changes, to see if there is a relationship with anthropogenic changes in the environment including conservation efforts and policy changes, to show the preferred nest type by the peregrine falcons through time, including the use of natural coastal or in-land, or manufactured structures, and to infer the direction of the recolonisation based on the location of nests of the pioneers.

Population Modelling

Population modelling uses mathematic equations applied to a given set of parameters to determine population dynamics of a species such as the growth rate and probability of extinction of the given species (Pavokovic and Susic, 2005). Through population modelling, the impact of factors affecting mating, mortality, productivity and population size on a given population of a species can be studied. It can also be used to determine the minimum number of individuals required for a population to survive and grow under pre-defined parameters. In this study, the primary population model used is a Population Viability Analysis (PVA), which provides the probability of extinction of a population, the mean population number of each year after the start of the simulation and the growth rate of a population under varying pre-defined parameters. Using PVA, it is possible to infer the expected trajectory of a population of a species placed under specific parameters set by the user (Boyce, 1992). By adjusting parameters, simulations can be created in which previous catastrophes can be tested on modern populations to get an understanding on whether or not the current population would be able to withstand the factors that caused the collapse of other or previous populations (Beissinger and McCullough, 2002). These simulations can also be used to predict the future of populations to see if under their current circumstances they would continue to grow, or if the population would plateau or experience extinction (Shaffer, 2019).

Population modelling has been previously used in the scope of Ornithology to determine the impact of potential conservation measures on declining populations, or to determine the number of individuals that would have to be released in a habitat to have a successful reintroduction program. An example of the former would be a study on conservation strategies for the Eurasian black vulture, (*Aegypius monachus*) , where it was determined that the current population would be at risk of extinction within the next 100 years (Dimitriou et al., 2021); however, through population modelling it was determined that conservation measures were needed, such as providing feeding stations and relocating some of the juveniles to a new area, while removing threats such as poisoning and wind farms, which once implemented would allow the black vulture population to grow and disperse over a greater range. PVA has also been used to inform the reintroduction of species; for example, PVA was used to determine the probability of extinction of the current population of bearded vultures (*Gypaetus barbatus*) recently reintroduced in the Alps, and whether the population would benefit from additional reintroductions (Schaub et al., 2009). It was concluded that the current population of bearded vultures would continue to grow without further reintroductions, and instead the resources should be diverted towards reintroducing bearded vultures to alternative ancestral locations where they are now extinct (Schaub et al., 2009).

In this thesis, the Sussex peregrine falcon population will be studied using population modelling and the records provided by SPS. It is expected that the records will provide sufficient detail to illustrate the pre- and post-population crash of the peregrines, the geographical distribution of the nesting sites, as well as evidence-based population trend of an unassisted recovery. The results of this study will help conservationists, practitioners and decision-makers understand the conditions that caused the population crash as well as its relatively quick recovery, and will serve as an example of how a population can recover from a local extinction and regain, or even surpass, previous population size. Furthermore, the results will serve as an example of an unassisted recolonisation which can only take place if the right conservation measures are already in place.

Aims and Hypotheses

What is the distribution, size and productivity of the current peregrine falcon population in Sussex?

The aim was to characterise the Sussex peregrine falcon population in terms of its distribution, current population size (number of birds or nesting pairs or nests) and productivity (the average number of eggs laid – and hatched – per active nest). It is expected that the current peregrine falcon population of Sussex will have a wide geographic distribution over Sussex, based on the observation of nesting sites across the county. It is expected that the current peregrine falcon population of Sussex will be much greater than any previous recorded years. It is expected that the current peregrine falcon population of Sussex will have a higher productivity than the previously recorded years.

What is the population structure and dynamics of peregrine falcons in the Sussex coast, and specifically comparing before and after the mid-20th century population crash?

The aim was to model the population size changes through time under different population scenarios, and to compare the population trends of the Sussex peregrine falcon population before and after the population crash. Based on records and observation provided by SPS, it is expected that the current peregrine falcon population of Sussex will have the highest growth rate compared to the previously recorded years. While doing a PVA, it is expected that the current peregrine falcon population of Sussex will have the lowest probability of extinction in comparison to the previously recorded years.

What is the chronology, rate and direction of recolonisation in coastal and inland sites?

As this species prefers cliffs, and the rock pigeon is the preferred prey, it is expected that the recolonising peregrine falcons of Sussex will establish their nests first in coastal areas, followed by inland sites and finally manufactured areas. If the new population was established from one or few pairs, it is expected that the rate of recolonisation of the peregrine falcons of Sussex will increase from 1990 up until 2016. Because the first observation of nesting pairs was in the south of Sussex, it is expected that the direction of recolonisation will begin from the south with the coastal sites being occupied first, and end towards the north, furthest from the coast.

Materials and Methods

Database

Population-level data on peregrine falcons from Sussex were collected by the SPS, including diaries and notes taken by Walpole-Bond, spanning from 1904 to 2016. This record contains information on nest establishment, active nesting sites, population size, young produced, eggs laid, site location, nest type and average eggs per pair. Site location is generally kept undisclosed (specific coordinates are not shown in this thesis) to prevent any illegal take.

Nest establishment is defined as the first year a new active nesting site is recorded since the recolonisation of Sussex. Active nesting sites refers to a specific site that has been observed with a nest being actively used by peregrine falcons. Based on this data it was possible to estimate range size, here referred as to the geographic distance (measured in kilometres) between the two most distant nests in southern England. Population size refers to number of birds, either single counts or as nesting pairs (males/female pair). Number of eggs laid may be different from number of young produced as some eggs might not have hatched, or young chicks may die before being counted. From number of eggs and number of young produced by active nests, it was possible to estimate 'productivity' calculated as the average number of eggs laid – and hatched –per active nest. The number of eggs laid and active nesting sites were used to determine 'egg productivity' calculated as the average number of eggs laid per active nesting site (regardless in this case of whether the eggs hatched). Nest type refers to where the nest is placed: on a coastal site (cliff), an inland site (a cliff, in a quarry, on a tree, on the ground) or on a manufactured site (artificial structure like pylons or buildings). Using this data, the productivity of specific years and productivity by nest type could also be determined.

The information provided by SPS was curated and arranged into an Excel file to allow downstream analyses using specialist software. The curation process involved the removal of any columns of data not relevant to either the population modelling or mapping procedure of the data analysis, streamlining the usage of the information in the specialist software used. This Excel file is available upon request to SPS (http://www.sussexperegrines.co.uk/).

Point maps

Point maps were used as graphical representations of the recolonisation, and were used to present the location, period of recolonisation and nest type. To visualise the recolonisation of Sussex, the recorded years of the recolonisation were separated into 7 groups: 1) 1990-1993, 2) 1994-1997, 3) 1998-2001, 4) 2002-2005, 5) 2006-2009, 6) 2010-2013 and 7) 2014-2017. The point maps used to create this graphical visualisation of the recolonisation were produced using the software QGIS version 3 (QGIS.org, n.d.). The peregrine falcon records include the coordinates of each nest, the year of establishment and the nest type. The coordinates were then imported into QGIS as point markers and a terrain map of southern England was then loaded. To present nests established within a period, point markers were placed on the nest location, and were coloured black, green or red to indicate if they were coastal, inland or manufactured, respectively. To indicate nests which were active, but had been established in a previous grouping, a grey marker was used. Through this method, the order, direction, and rate of recolonisation could be seen from the location of the points established in each grouping and the number of nests being established in each grouping.

Heatmaps

Heatmaps were used as graphical representations of the data to present the density of nests. In this case, heatmaps of established nests expressed how many recorded nests are nearby (i.e., density of nests in the vicinity). To visualise nest density through time, several years were selected to represent time periods before the population crash ('1912' and '1936'), before and early on during the persecution and population crash ('1946' and '1954'), and post-population crash ('1995' as recent recovery time and ‘2016’ – the most recent population survey). The heatmaps used to create a comparison between these years (i.e., 1912, 1936, 1946, 1954, 1995 and 2016) were produced using the software QGIS version 3 (QGIS.org, n.d.). The peregrine falcon records include the location of the nests alongside their coordinates for each year. The coordinates were then imported into QGIS as point markers and a terrain map of southern England was then loaded. These point markers were then converted to a heatmap using the ‘Heatmap’ tool in QGIS. The radius of peregrine falcon territory was obtained as the average reported from several studies revised in Ratcliffe (2008). A radius of 32.19 kilometres was used, and this value was applied for each year so the maps could be readily compared.

Statistical analysis

Statistical analysis has been used throughout this paper in the form of Pearson correlation coefficient, linear regression, 2 sample t-test and Chi-square goodness-of-fit test. The usage of these tests allowed any associations between variables to be identified. To perform these tests, Minitab 22 was used (Minitab, 2023). To run these tests, data was taken from the curated excel spreadsheets acquired from SPS and inserted into the Minitab spreadsheet. The desired tests were selected in Minitab through the use of drop-down boxes, and the variables for each test were input into the dialog box. This process provided the results of the statistical analysis along with associated graphs. The data input into Minitab from the excel spreadsheets was year, number of active sites, number of young produced, nest type and productivity.

Population Viability Analysis

The peregrine falcon population of Sussex was modelled using Vortex version 10 (Lacy and Pollak, 2022), which is a simulation program for population viability analysis (PVA). To run the analyses, a set of parameters were compiled (Table 1), which were then entered in Vortex to create a PVA. All parameter fields in Vortex 10 were input using real-world values from literature where possible, however, when no supporting literature could be found for a parameter, default parameters were used as outlined in the Vortex 10 user manual (Lacy, Miller and Traylor-Holzer, 2021). The parameters used within the PVA were acquired through both primary literature and the records provided by SPS for this study.

The default parameter simulation created was based on data from 2016, which is the most recently available data provided by SPS. The chosen length of the simulation was 50 years, with the final year being the calendar year 2066. The tests were run over 1000 iterations to ensure accuracy of results. A default parameter simulation is required in this study as it provides insight into the dynamics of how a minimally impeded population, like that of 2016, would change over time, allowing the impact of factors affecting the population dynamics to be measured and visualised, using the default parameters as a baseline.

To model the populations at different times representing different levels of persecution, habitat degradation and environmental pollution, three specific populations were chosen being '1912' (pre-crash and pre-intensive persecution and environmental pollution, and the highest population size based on records), '1941' (pre-crash but persecuted), and '2016' (the most recent record after the recolonisation). The 1912 population represents a typical peregrine falcon population prior to the population crash and before there was intense persecution during WW2 and environmental pollution due to organochlorine pesticides; moreover, this year shows the highest number of birds present in Sussex before the crash. The 1941 population was the final year in which young were produced once the crash of the Sussex population was underway. 2016 represents the modern population of Sussex, which has benefited by changes in the legislation and conservation efforts.

The parameters inputted into Vortex fall under four main categories: 1) reproductive system, 2) mortality rates, 3) initial population size, and 4) carrying capacity. Reproductive system of the peregrine falcon was defined as long-term monogamy. The factors inputted were Age of first offspring for both male and female, maximum age of reproduction for both sexes, the maximum life span of the peregrine falcon, the number of broods per year, the maximum number of offspring per brood, and the clutch sex ratio of peregrine falcons. Mortality rates cover the percent chance of mortality at different life stages of the peregrine falcon for each sex. For Vortex, extinction of a population is reached when ‘Only one sex remains’ rather than when zero individuals are present in the population. The initial population sizes for the three population sets were 47, 11 and 120 peregrine falcons for the populations 1912, 1941 and 2016, respectively, with the population sex ratio being equal to match the natural clutch sex ratio, as their actual genders were unknown. The population sizes were based on SPS records for the Sussex peregrine falcons observed and counted on those years. The ages of all the male and female samples were decided through a ‘stable age distribution’ provided by Vortex, as the actual ages of the birds were unknown. The carrying capacity for Sussex was calculated by taking the area of Sussex and dividing it by the average nesting territory of peregrine falcons, and then multiplied by two as a nest can contain a pair of adult birds, leading to a carrying capacity of 1008. ((3783.973/7.511) x 2 = 1007.581). As the peregrine falcon population has increased in recent years, and typical nest availability on cliffs has likely decreased, peregrine falcons have been witnessed nesting almost indiscriminately, for example on trees, pylons, buildings and on the ground, as long as they were not too close to another pair of peregrine falcons. This indiscriminate nesting behaviour suggests that the whole of Sussex could be occupied by peregrine falcons, with the key factor being the distance from the nearest peregrine falcon nest.

To examine how the populations would have looked if the factors causing the crash were not occurring, the default parameters shown in Table 1 were applied. These are the modern-day conditions since a ban on persecution, egg-collecting and usage of organochlorine pesticides.

Table 1. Peregrine falcon organismal and population parameters used in Vortex for population viability analyses.

Parameter	Reference	Value
Reproductive system	(Robinson, 2005)	Long-term Monogamous
Age of first offspring females	(Robinson, 2005)	2

Age of first offspring males	(Robinson, 2005)	2
Maximum age of female reproduction	(Robinson, 2005)	21
Maximum age of male reproduction	(Robinson, 2005)	21
Maximum Lifespan	(Robinson, 2005)	21
Maximum number of broods per year	(Robinson, 2005)	1
Maximum number of progeny per year	(Robinson, 2005)	5
Clutch Sex ratio	(Burnham, W., Sandfort, C. and Belthoff, J.R., 2003)	50%
% adult females breeding	(Lacy, R.C., P.S. Miller, and K. Traylor-Holzer, 2021)	80%
Survival 0-1	(Craig, White and Enderson, 2004)	0.544
Survival 1-2	(Craig, White and Enderson, 2004)	0.67
Survival 2+	(Craig, White and Enderson, 2004)	0.8
Initial Population size (2016, 1941, 1912)	(Sussex Peregrine Study, n.d)	120/11/47
Carrying capacity	(This study)	1008

One of the goals of this study was to identify how different populations of peregrine falcons, witnessed throughout the recorded history, would react to the different conditions which have been documented over their history, such as times of no productivity, or increased persecution. To examine the effects of these factors, the default parameters seen in Table 1 were changed to mimic that of the condition being tested. To replicate the conditions of years in which productivity was 0, the percent of adult females breeding was set to 0% as this would end the production of eggs and young. To examine the effects of persecution, a population harvest was conducted in which 1 female and 1 male were removed on a yearly basis for the duration of the simulation. These factors were then combined to represent the conditions witnessed over the crash of the peregrine falcon population. Another factor measured independently on the modelled populations was the effect of immigration. To measure the impact of immigration on the different Sussex populations, a population supplementation was used in which 1 male and 1 female were added to each population yearly for the 50-year duration of the simulation.

For the annual persecution, 1 male and 1 female were chosen due to the documented historical persecution by JWB and limitations in the PVA model. From the historical records, it is documented that JWB shot six falcons personally from 1904-1956, although other individuals may have shot additional birds; however, this it is not thought to be a significant number of deaths, as each nest was commonly reoccupied annually over the recording period. The actual number of birds persecuted in Sussex each year would have been lower than one male and one female annually but due to model limitations this was the lowest value that could be chosen. To simulate persecution, a 'harvest' function was used which required a whole number to be chosen to be annually removed from the population pool. This meant that a decimal could not be used to represent less than one bird of each sex being removed each year. Due to these compounding factors, it was decided that 1 male and 1 female would be used as it was the closest possible value to the number of bird shots annually, while still providing insight on the effect of persecution.

For the annual supplementation of the population through immigration, 1 male and 1 female were chosen due to the dispersal patterns of peregrine falcons in the UK, the documented local populations at the time and limitations in the PVA model. The natal dispersal of peregrine falcons in the UK has been recorded as males averaging 44 km, while females average 117 km, suggesting the furthest location peregrine falcons are likely to be emigrating to Sussex from is the south of England (southeast, south central and southwest). Ratcliffe documented the populations of peregrine falcons in the UK from 1990-1995, in which the south of England had one of the lowest breeding populations. Furthermore, when examining the population collapse, the southeast and southwest of England had the most drastic reduction in percentage of occupied territories. Subsequently, these compounding factors lead to the conclusion that the minimum number of males and females should be supplemented into the population on a yearly basis. Due to these limitations in the model, the lowest yearly supplementation rate was used in the simulation, which is the addition of 1 male and 1 female each year from year 1 to year 50.

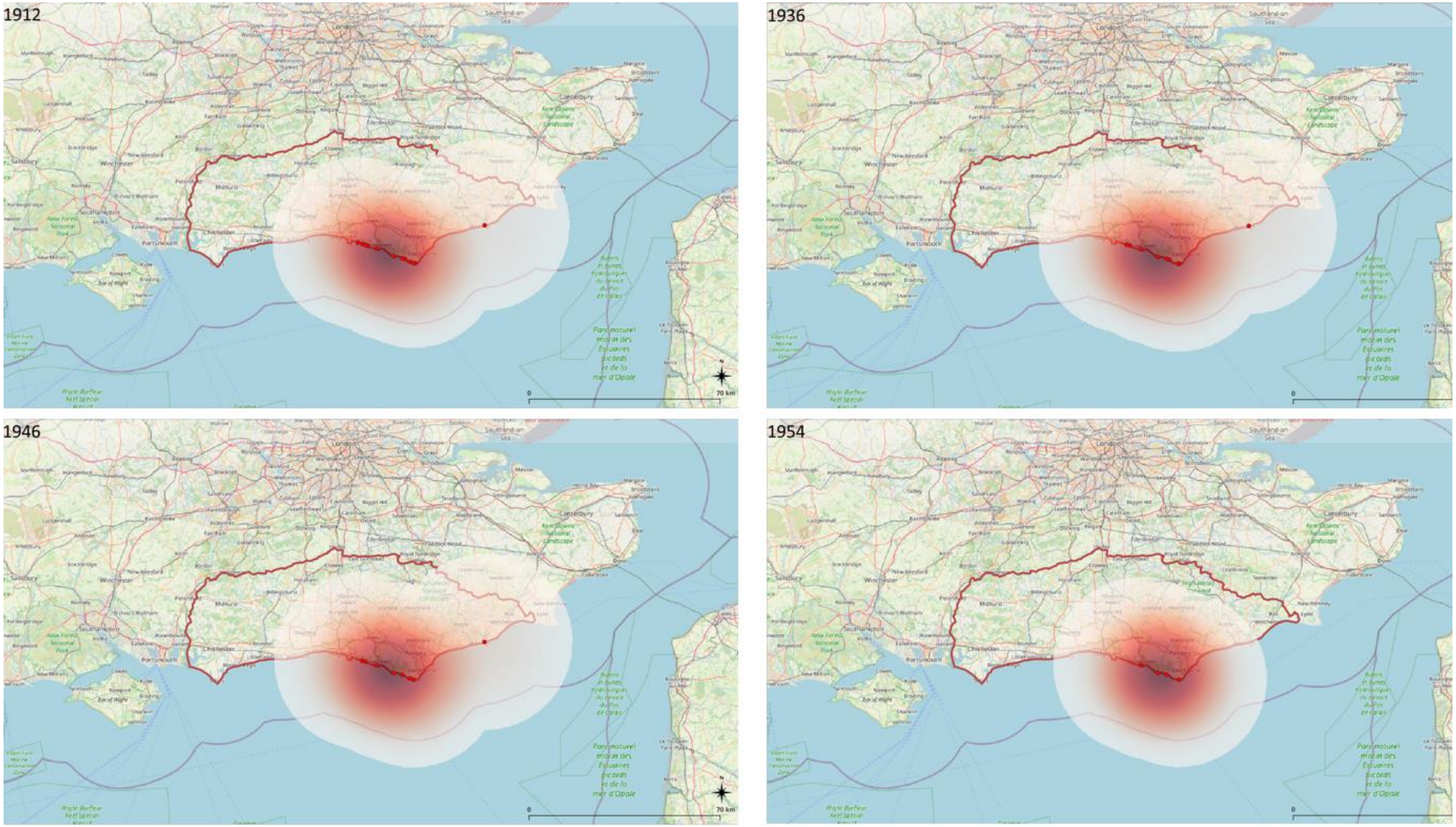
Results

Sussex peregrine falcons

The SPS dataset, including Walpole-Bond's diaries and SPS observations, provided a comprehensive representation of the peregrine falcon population throughout the 20th century until 2016. Based on the geographic distribution of the nests, and the distances from the two most extreme nest sites in southern England, it is possible to observe a change in peregrine falcon nest range through time (Table 2). In 1912 there were 12 recorded nests with a range of 47.2 km, spanning from Hastings to Brighton, by 1936 there were 9 recorded nests with a range of 45.5 km, reaching from Hastings to Brighton, and by 1946 there were 8 recorded nests covering a range of 45.5 km spanning from Hastings to Brighton; therefore, between 1912 and 1946 there was only a slight reduction in range (Fig. 1). In 1954 there were 4 active nests spanning 15.0 km and ranged from Eastbourne to Brighton; this was a marked reduction in range and active nests in comparison with previous years (Fig. 1). The peregrine falcon was extirpated from the area until 1990, when new nests were found and recorded. By 1995, after the population had 5 years to recolonise Sussex, the range was nearly twice as much as in 1912, showing 9 active nests and reaching a range of 97.5 km spanning from Chichester to Hastings (Fig. 1). By 2016, as the population continued to grow, there were 54 active nests and the range reached 114.3 km spanning from Petersfield to Rye (Fig. 1), almost 2.5 times larger than the 1912 population and more than 7.5 times larger than the 1954 population.

Table 2. Number of active nest sites and geographic distance measured between the two furthest nests, recorded as range, on specific years.

Year	Active Nests	Range (kilometres)
1912	12	47.2
1936	9	45.5
1946	8	45.5
1954	4	15.0
1995	9	97.5
2016	54	114.3


1912
1936
1946
1954
0
70 km

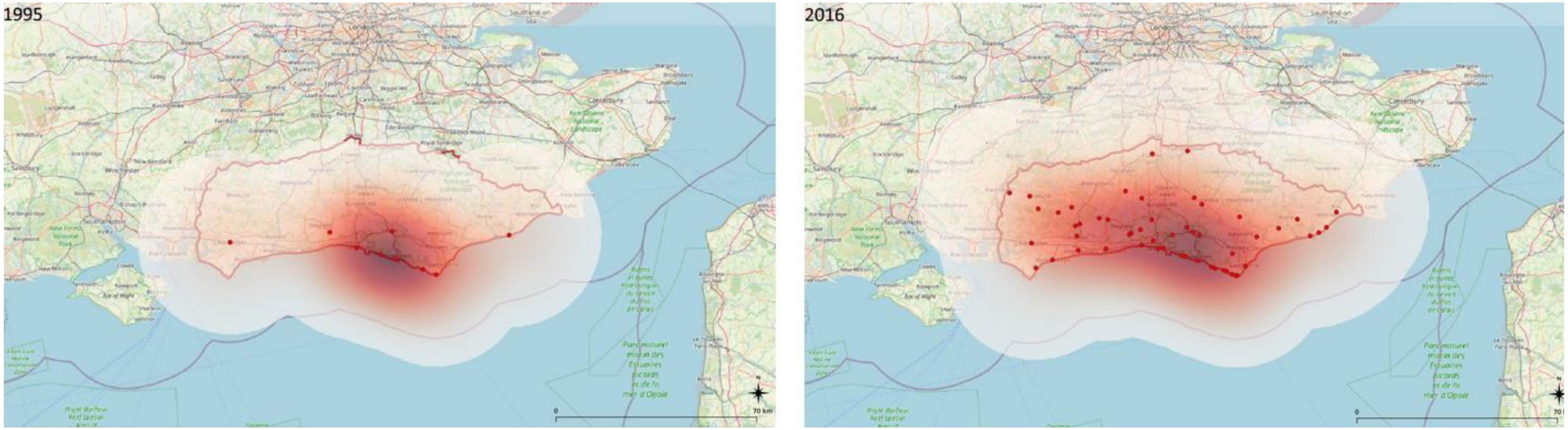


Figure 1. Geographic distribution of nesting territory of peregrine falcons in southern England along with point markers showing approximate location of nests at six selected years: 1912, 1936, 1946, 1954, 1995, and 2016. The red border indicates the boundary of Sussex.

There was an average of 7.39 active nesting sites in the pre-clash peregrine falcon population from 1904-1922. Although the number of active nesting sites fluctuated on a yearly basis until 1952, when 0 active nests were recorded, it is apparent that peregrine falcons were still present and trying to nest in the area regardless of the level of persecution in early 20th century and during the early use of pesticides (Fig. 2, Table 3). However, the number of young produced in early 20th century, with an average of 6.444 young produced between 1904-1922, peaked in 1912 but later declined until reaching zero eggs hatching between 1922 to 1931, during the time of heavy egg collection. From 1952, no active nests were recorded until 1989, excluding one observation in 1963 which may be anomalous data. From 1989, the number of nesting sites grew steadily, and greatly surpassed pre-crash active nest site numbers by the late 1990s. A similar trend was followed in egg productivity, with early recolonisation stages showing only a few young being produced and surpassing pre-crash numbers by late 1990s-early 2000s. There was an average of 24.39 young produced from 1989-2016, almost 4 times the average number of young produced in the 1904-1922 period (Fig. 2, Table 3).

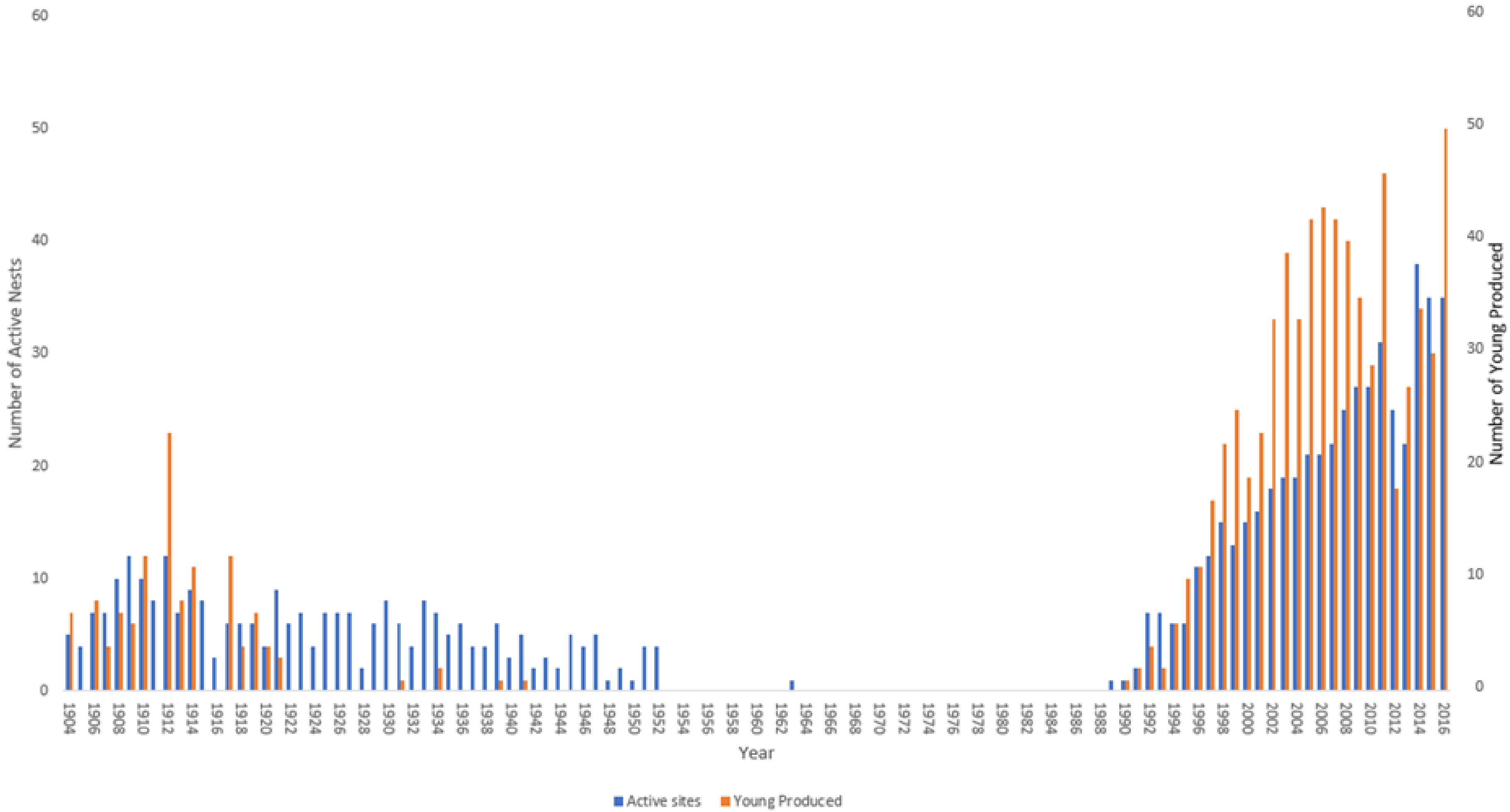


Figure 2. Number of active nesting sites of peregrine falcons in Sussex and number of young produced between 1904-2016.

Table 3. Average number of active nests and the average number of young produced in the defined periods of Sussex's peregrine falcon population.

Time Period	Average Number of Active Nests	Average Number of Young Produced
1904-1922	7.39	6.44
1923-1952	4.68	0.16
1953-1988	0.03	0.00
1989-2016	17.75	24.39

The pre-crash population, spanning from 1902-1952, had a declining number of active nests, with a rate of change of -0.636 each year (Fig.3, Table 4). The ANOVA of this data reported a p-value of 0.000, which in the software Minitab, indicates a value less than 0.0005 (Minitab,2023). This p-value indicates that there is a statistically significant association between the number of active nests and time over the pre-crash period. Despite the variation in active nesting sites, with some years increasing and others decreasing, the general trend over this period was that of a declining value. In this pre-crash period this declining trend could be linked to the persecution of the species and the reduced adult population due to the extensive egg collecting preventing new mature PFs to enter the pool. Despite the declining number of active nesting sites, a year with no active nesting sites was not seen until the post-crash period which spanned from 1953-2016.

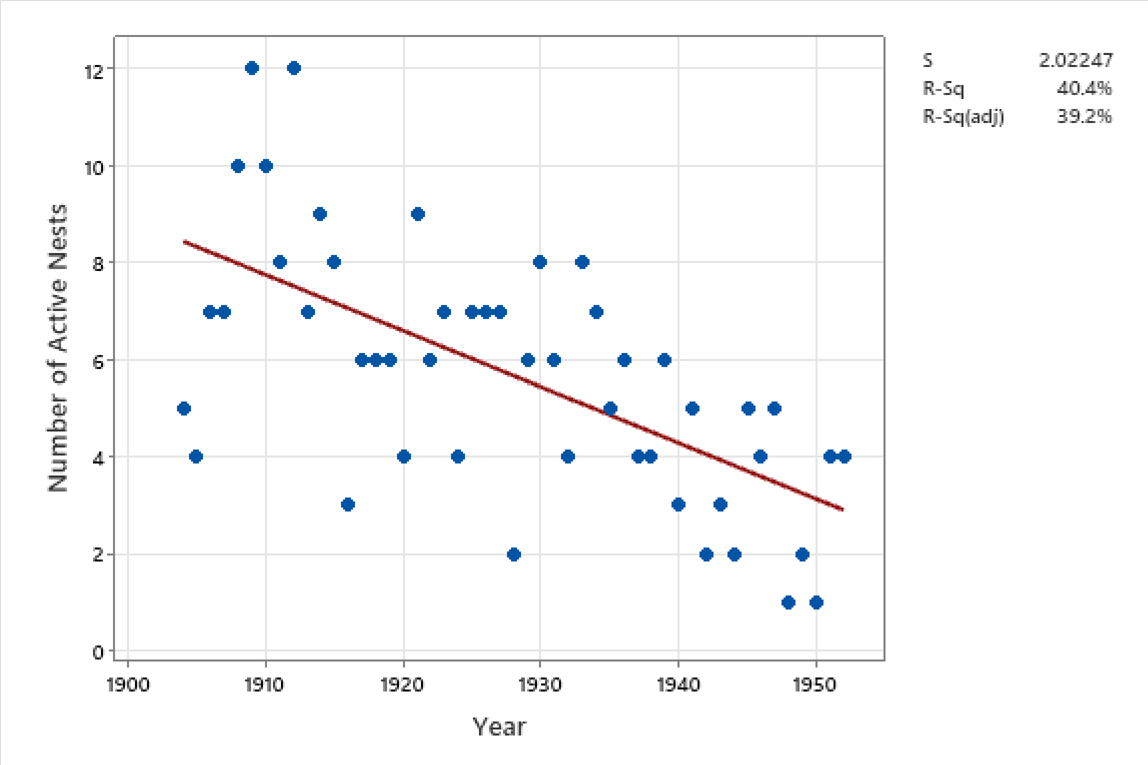


Figure 3. Linear regression of the number of active nests against time of the pre-crash Sussex population.

The post-crash population, spanning from 1953-2016, had a growing number of active nests, with a rate of change of 0.851 each year (Fig.4, Table 4). The ANOVA of this data reported a p-value of 0.000, which in the software Minitab, indicates a value less than 0.0005 (Minitab,2023). This p-value indicates that there is a statistically significant association between the number of active nests and time over the post-crash period. The number of active nesting sites during this period is generally seen continually growing or maintaining the number of nesting site, with only 8 of the 63 years seeing any decrease in number of active nesting sites. The growth seen in this period is due to the conservation efforts put in place for the species and the availability of nesting sites. As conservation measures were put in place within this period, the population was seen to be successfully growing due to the increased productivity and survival of adults, thus meaning there were more mature PFs to establish and occupy nesting sites. In addition to the increasing number of mature PFs, there was also a high number of available nesting sites in Sussex due to the lack of PFs in Sussex at the start of this recorded period. Additionally, with the creation of many large, manufactured structures in comparison to the pre-crash population, there are now a higher number of viable nesting sites in Sussex than previously seen.

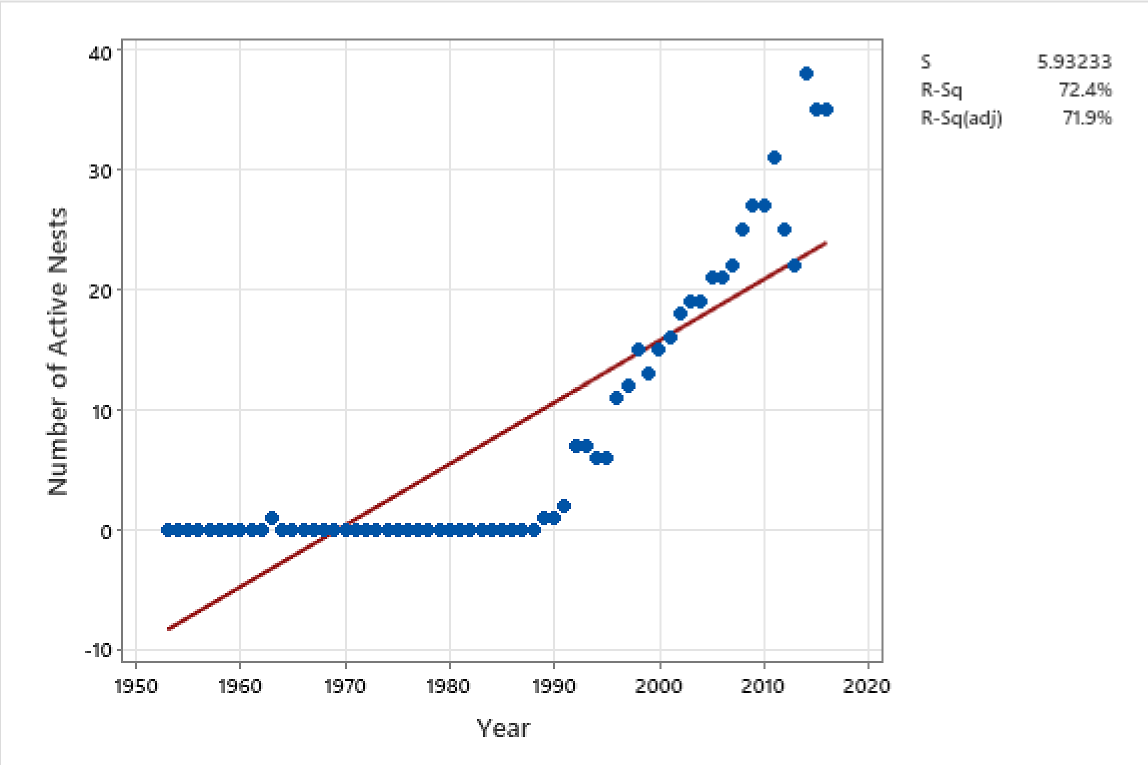


Figure 4. Linear regression of the number of active nests against time of the post-crash Sussex population.

The results of a two-sample t-test between the pre-crash and post-crash populations provided a p-value of 0.150, indicating that the number of active nests does not significantly differ between the two time periods. The mean for the two groupings were 5.67 and 7.80 for pre-crash and post-crash respectively. The post-crash population has many years with 0 active nesting sites, greatly lowering the mean and thus making it not significantly different to the pre-crash population.

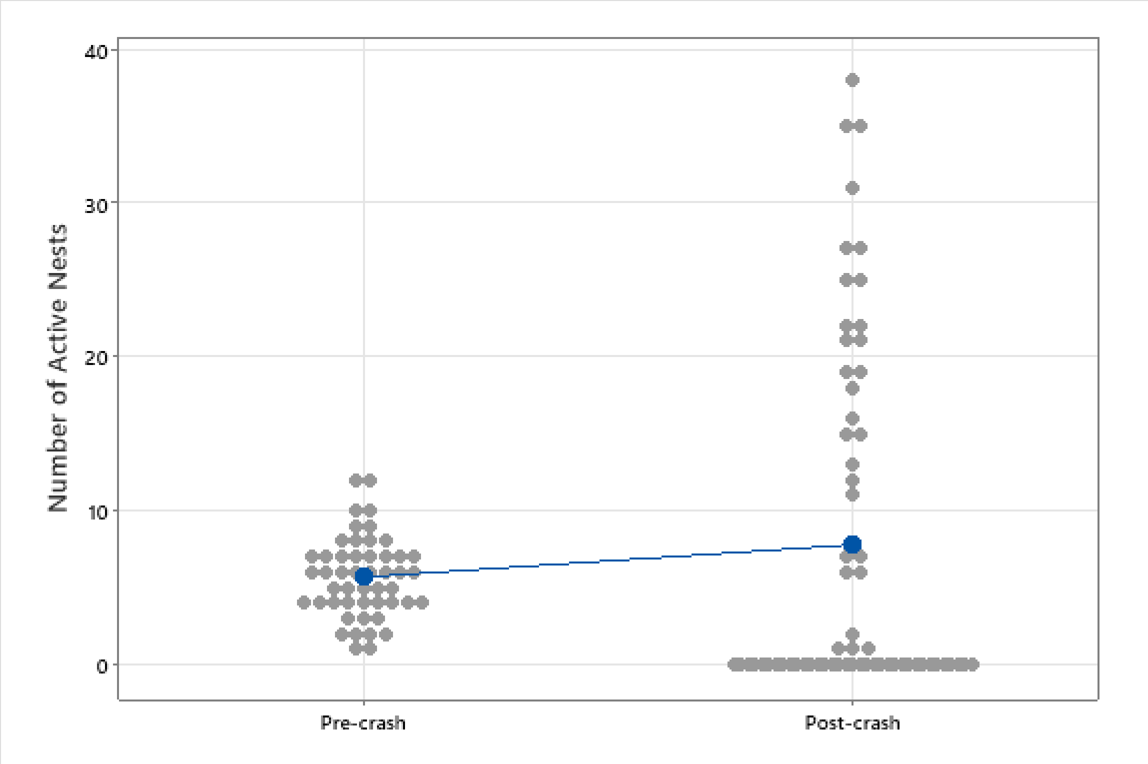


Figure 5. Number of active nests each year for the pre-crash and post-crash peregrine falcon populations of Sussex.

The pre-crash population, spanning from 1902-1952, had a declining number of young produced, with a rate of change of -0.567 each year (Fig.6, Table 4). The ANOVA of this data reported a p-value of 0.000, which in the software Minitab, indicates a value less than 0.0005 (Minitab,2023). This p-value indicates that there is a statistically significant association between the number of young produced and time over the pre-crash period. This period is inconsistent in the initial decades with the number of young produced ranging from 23-0, likely influenced from JWBs sporadic egg collection throughout this period. From 1922-1952, despite the lack of organochlorine poisoning at this time, there was consistently years with no productivity, with just 4 years producing young. The cause of this lack of productivity is due to JWB starting to collect every egg from every known nesting location. This lack of productivity then continued into the 1980s due to the organochlorine crisis causing a drastic reduction in productivity.

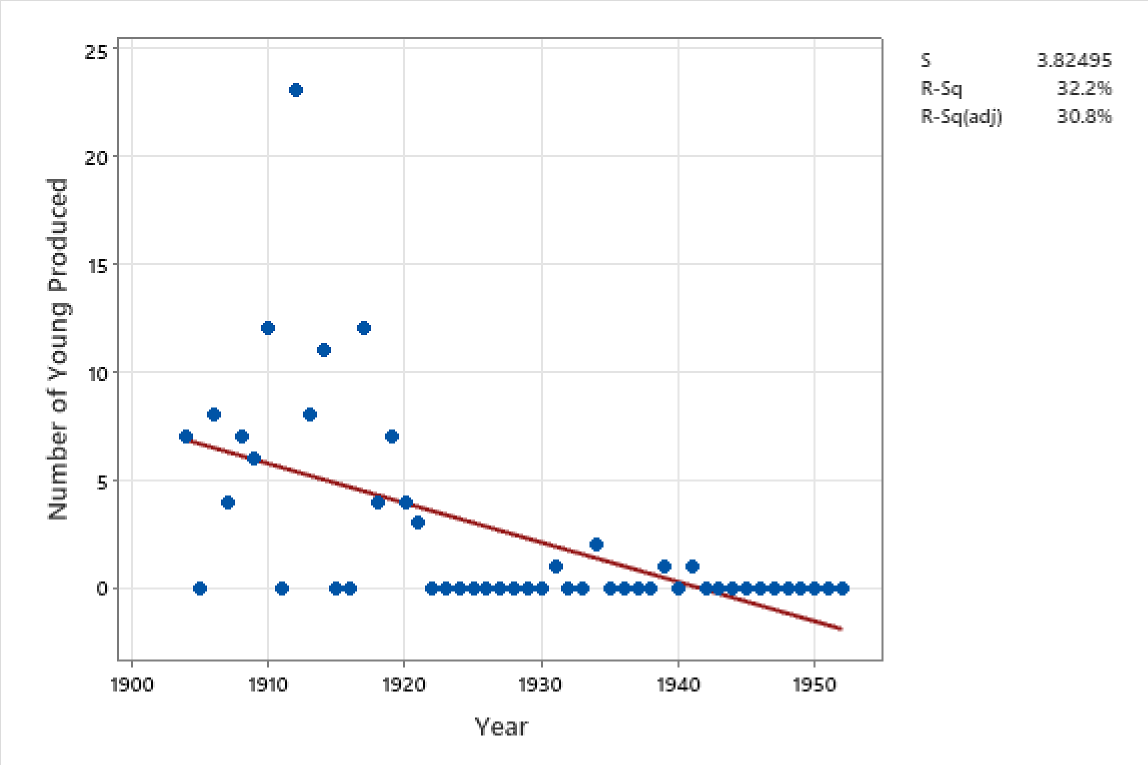


Figure 6. Linear regression of the number of young produced against time of the pre-crash Sussex population.

The post-crash population, spanning from 1953-2016, had a growing number of young produced, with a rate of change of 0.813 each year (Fig.7, Table 4). The ANOVA of this data reported a p-value of 0.000, which in the software Minitab, indicates a value less than 0.0005 (Minitab,2023). This p-value indicates that there is a statistically significant association between number of young produced and time over the post-crash period. The number of young produced during this period is generally seen to be growing, however, during some of the later years of the data, some substantial dips in number of young produced can be seen. These dips could be due to unaccounted factors such as a period of inclement weather causing egg failure or a lower number of prey availability that year. The growth seen in this period is due to the conservation efforts put in place for the species and the availability of nesting sites. As conservation measures were put in place within this period, the population was seen to be successfully growing due to the increased survival of adults, thus meaning there were more mature PFs to produce offspring. In addition to the increasing number of mature PFs, there was also an increase in the number of active nesting sites due to the increased availability of nesting sites in this period. Subsequently, more nests were established than in the pre-crash population, allowing more young to be produced overall.

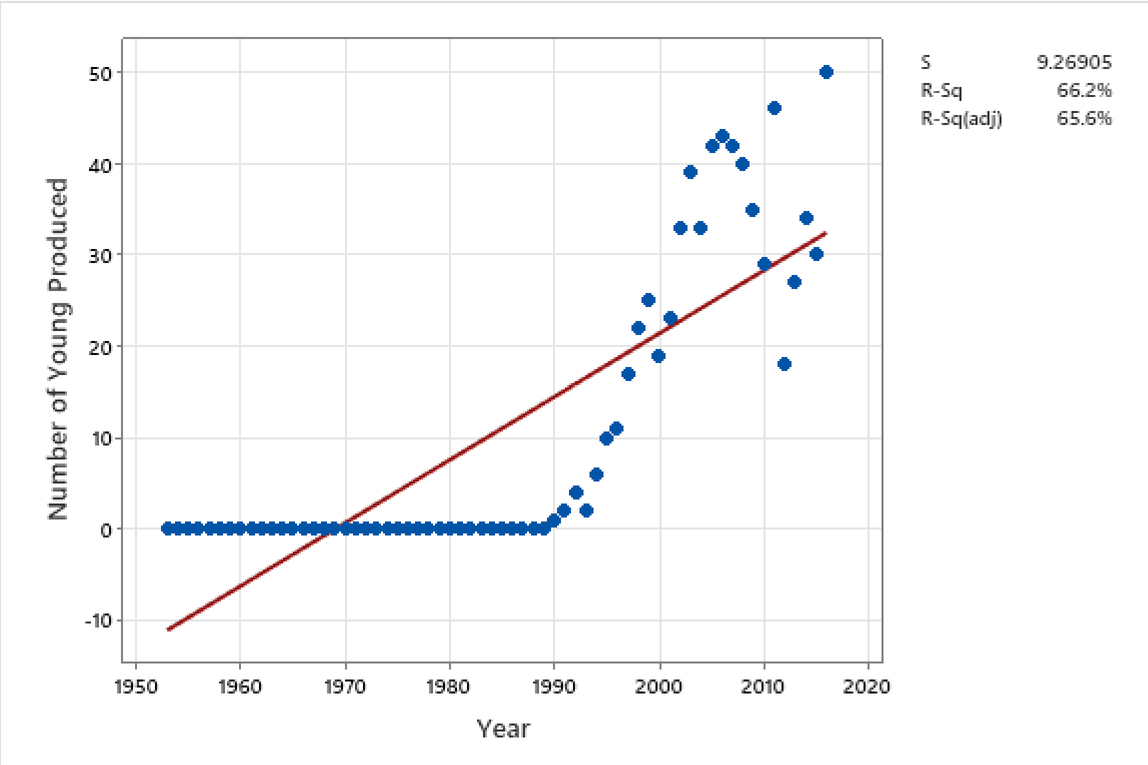


Figure 7. Linear regression of the number of young produced against time of the post-crash Sussex population.

The results of a two-sample t-test between the pre-crash and post-crash populations provided a p-value of 0.000, indicating that the number of young produced significantly differs between the two time periods. The means for the two groupings were 2.47 and 10.7 for pre-crash and post-crash respectively. This is due to the conservation efforts put in place, allowing the productivity of the PFs to greatly increase, alongside the number of mature PFs producing eggs greatly increasing.

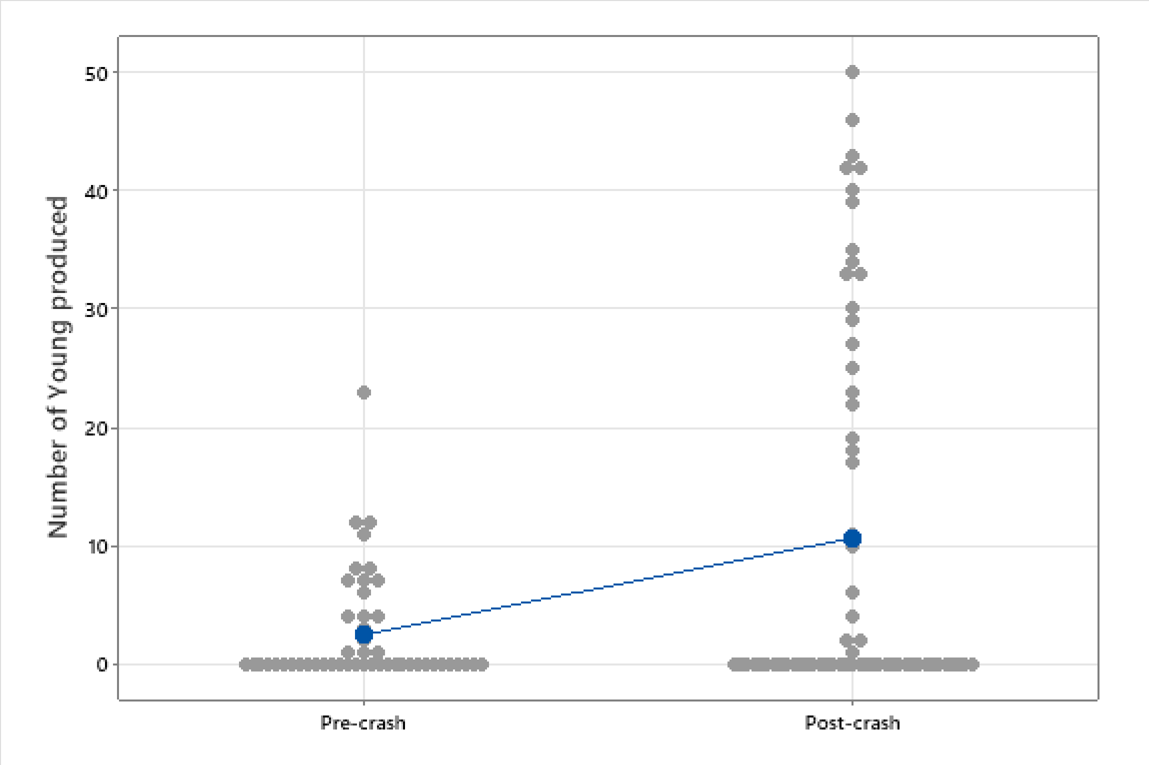


Figure 8. Linear regression of the number of young produced against time of the post-crash Sussex population.

Table 4. Correlation of the active number of nests and the number of young produced with time, for the pre and post-crash Sussex peregrine falcon populations.

Time Period	(1)-Number of Active Nests Correlation with Time	ANOVA P-value of (1)	(2)-Number of young Produced Correlation with Time	ANOVA P-value of (2)
Pre-crash (1903-1952)	-0.636	0.000	-0.567	0.000
Post-crash (1953-2016)	0.851	0.000	0.813	0.000

There was an average of 20.94 eggs laid from 1904-1922 (Fig. 9). The number of eggs laid then fluctuated until 1952, in which 0 eggs were laid. No more eggs were recorded in the area until 1990. From 1990-2003, the number of eggs laid increased to an average of 10.27 eggs laid. Although there appears to be an upward trend in number of eggs laid since 1990, the average is still about half of what it was in the pre-crash population.

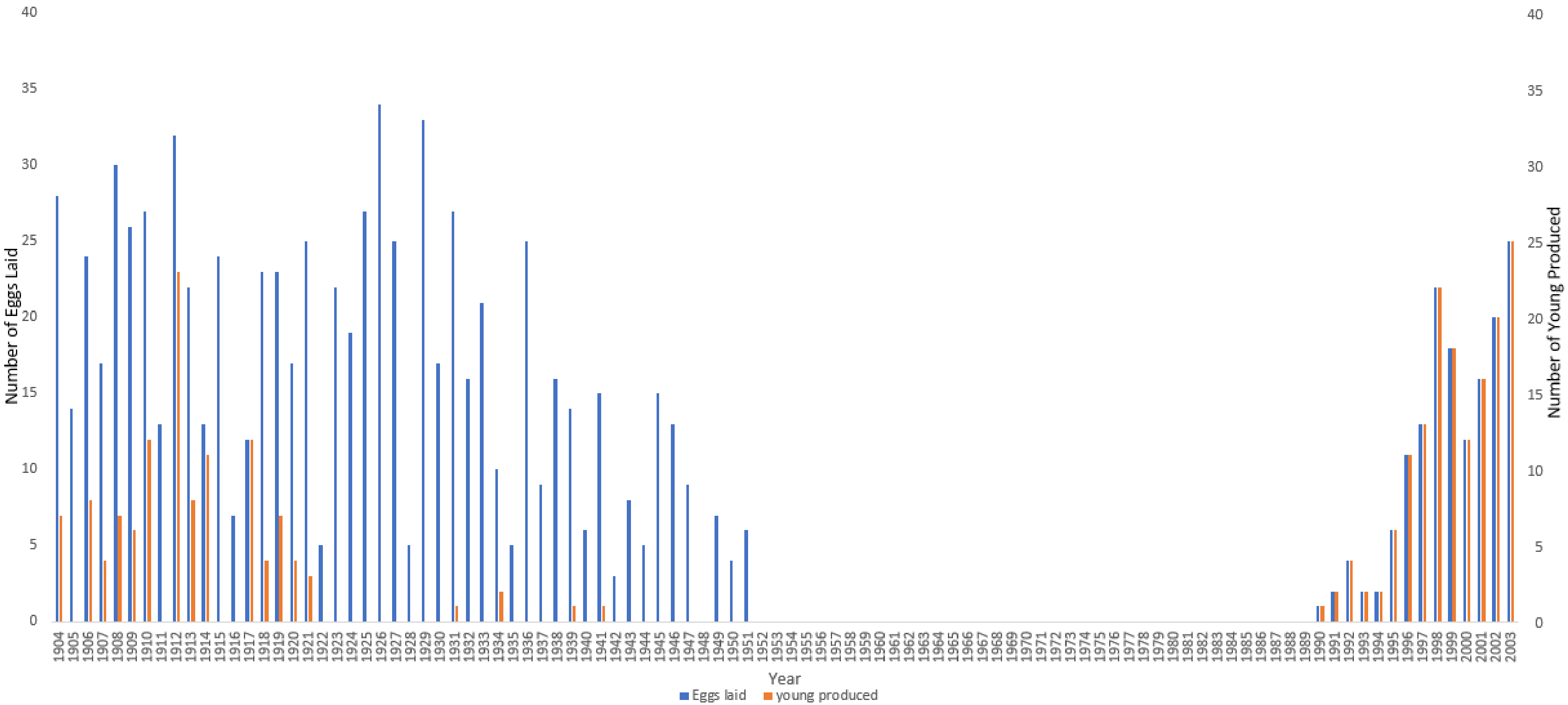


Figure 9. Number of Sussex peregrine falcon eggs laid, and the number of young produced from 1904-2003.

Based on the number of eggs laid – and hatched – on average per nest, there was an apparent change in productivity through the years 1904 to 2016 (Fig. 10). From 1904-1922 the average productivity was 0.831 eggs per nest. From 1922 until 1990, only four years produced young, lowering the productivity to 0.012 eggs per nest. After 1990, during the post-population crash, nest productivity rose quickly and had an average of 1.293, higher than before the population crash.

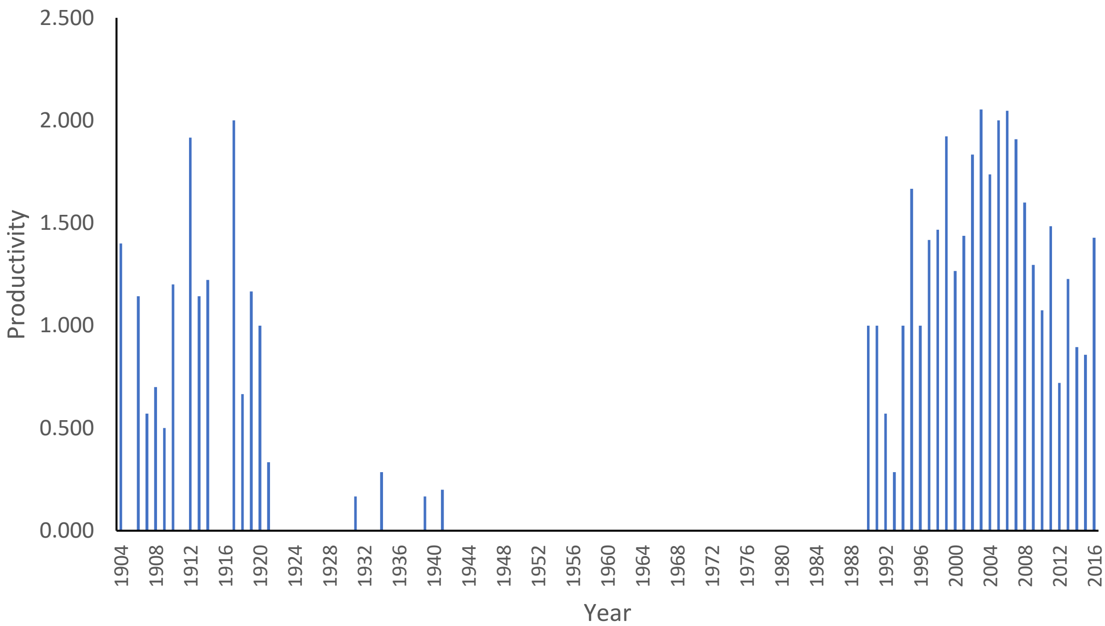


Figure 10. Productivity of peregrine falcons in Sussex from 1904 to 2016. Productivity is expressed as the average number of eggs laid -and hatched- divided by the number of active nests.

The records kept by the SPS allowed for the visualisation of the recolonisation of southern England since 1990 and indicate the nest types being used by the colonisers (Fig. 11, Fig. 12). In total, the total number of peregrine falcon nests since recolonisation was 55, including 13 coastal sites, 19 inland quarries and 23 manufactured sites. From 1990 to 1993 there were 8 active nests, mostly coastal, but also 2 nests in manufactured structures and 1 nest inland. In subsequent years, as more breeding pairs were present in the area, more coastal, inland and manufactured nests were recorded. No further new nests were established from 2001 to 2016 on coastal sites. In 2017, however, one more additional active coastal nesting site was established (observation made by SPS). Through time, the number of coastal nest sites reached a maximum of 13, and by 2008 they were surpassed by inland nests, and by 2012 they were surpassed by manufactured nests (Fig. 11, Fig. 12).


1990-1993


1994-1997


1998-2001


2002-2005

Legend

- Coastal Nest Established in the Current Four-Year Grouping
- Active Coastal Nest Established in a Previous Four-Year Grouping
- Inland Nest Established in the Current Four-Year Grouping
- Active Inland Nest Established in a Previous Four-Year Grouping
- Manufactured Nest Established in the Current Four-Year Grouping
- Active Manufactured Nest Established in a Previous Four-Year Grouping
- Abandoned Nest Established in a Previous Four-Year Grouping

Figure 11. Point maps showing the location of peregrine falcon nest sites established in each four-year period and their subsequent usage or abandonment in the following four-year periods after the recolonisation of Sussex in 1989. The seven four-year periods are 1990-1993, 1994-1997, 1998-2001,2002-2005, 2006-2009, 2010-2013 and 2014-2017. In the final panel, a legend depicts the type of nest and whether they were established in the current four-year period, or in a prior four-year period. The red border indicates the boundary of Sussex.

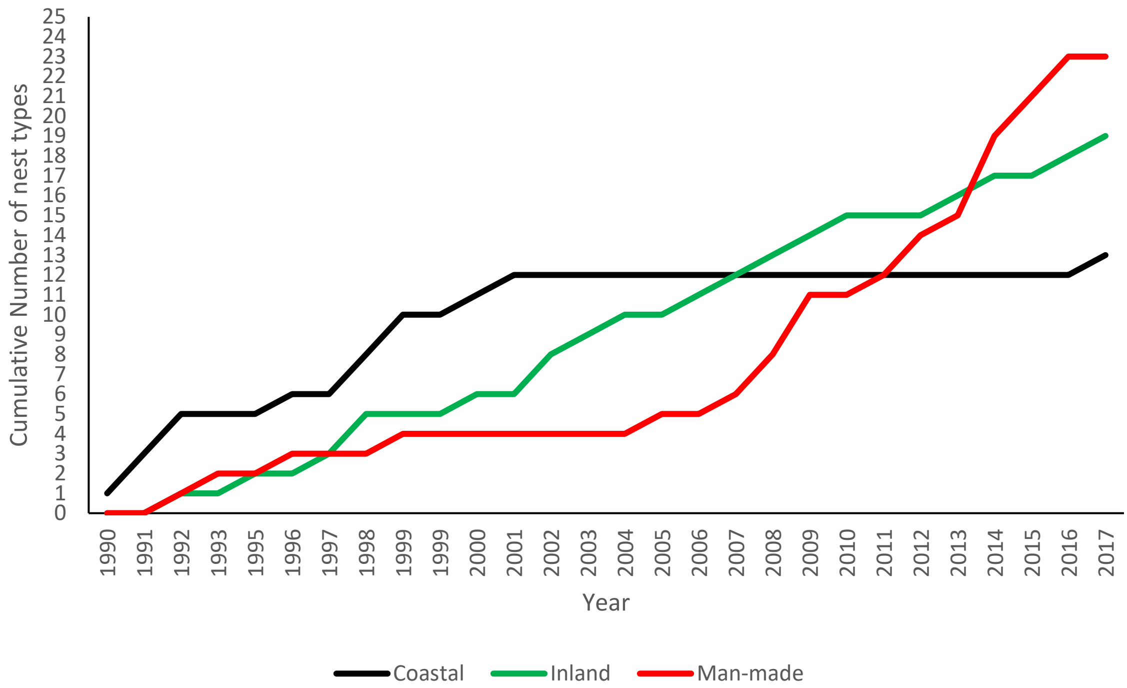


Figure 12. Cumulative number of peregrine falcon nest types (coastal cliffs, inland and manufactured sites) in Sussex since its recolonisation.

Coastal sites had the highest initial rate of recolonisation, with a rate of 1.09 nests established per year from 1990-2001; however, this greatly plateaued as no further nests were established from 2001 to 2016 on coastal sites. The results indicate that coastal sites were the most productive nest type with a productivity of 1.667 in 2016 (Table 4). Establishment of inland nests maintained a steady increase since the recolonisation Sussex with an average rate of 0.7 inland nests per year from 1990-2017. Inland sites had a nest productivity of 1.429 eggs per nest in 2016 (Table 4). manufactured sites were slow to be established in the initial recolonisation phases, with 5 nests being established from 1990-2004. But from 2005-2017, the number of manufactured nests increased, reaching 23, which averaged 1.92 nests per year during this period; however, manufactured sites proved the least productive overall, with a nest productivity of 1.25 in 2016 (Table 4). Despite the variations seen between each nest type, the goodness-of-fit test has determined that the number of active nests, the number of young produced and the productivity all fail to reject the null hypothesis, confirming that there is not a statistically significant difference between each for variable for the three habitats.

Table 5. Productivity of each nest type of peregrine falcons in Sussex being actively used in the year 2016, and the goodness-of-fit of each variable for the differing habitats

Nest type	Active nests	Young Produced	Productivity
Coastal	9	15	1.667
Inland	14	20	1.429
Manufactured	12	15	1.25
Chi-Square P-value	0.000	0.000	0.000

Population Viability Analysis

The PVA of Sussex peregrine falcons under default parameters indicated the survival of the 1912 and the 2016 populations, while the 1941 population had a high chance of extinction (Fig. 13). The PVA for the 1912 population indicated that the probability of extinction was 0.000, with a mean growth rate (r) of 0.085, and a standard deviation (SD(r)) of 0.121. By the 50th year of the simulation, the mean number of individuals in this population was 951.10, showing an increase of 2023% from the initial population size of 47 individuals. The PVA for the 1941 population indicated that the probability of extinction was 0.626, with an r = -0.006 and an SD(r) = 0.208, with a mean time to go extinct of 24.39 years (SD = 12.51). In the 1941 population, by the 50th year of the simulation, the mean number of individuals both extant and extinct was 34.12, showing an increase of 310% from the initial population size of 11 birds. The PVA for the 2016 population indicated that the probability of extinction was 0.000 with an r = 0.1028 and an SD(r) = 0.00. By the 50th year of the simulation, the mean number of individuals in this population was 992.62, showing an increase of 827%, from the initial population size of 120 birds.

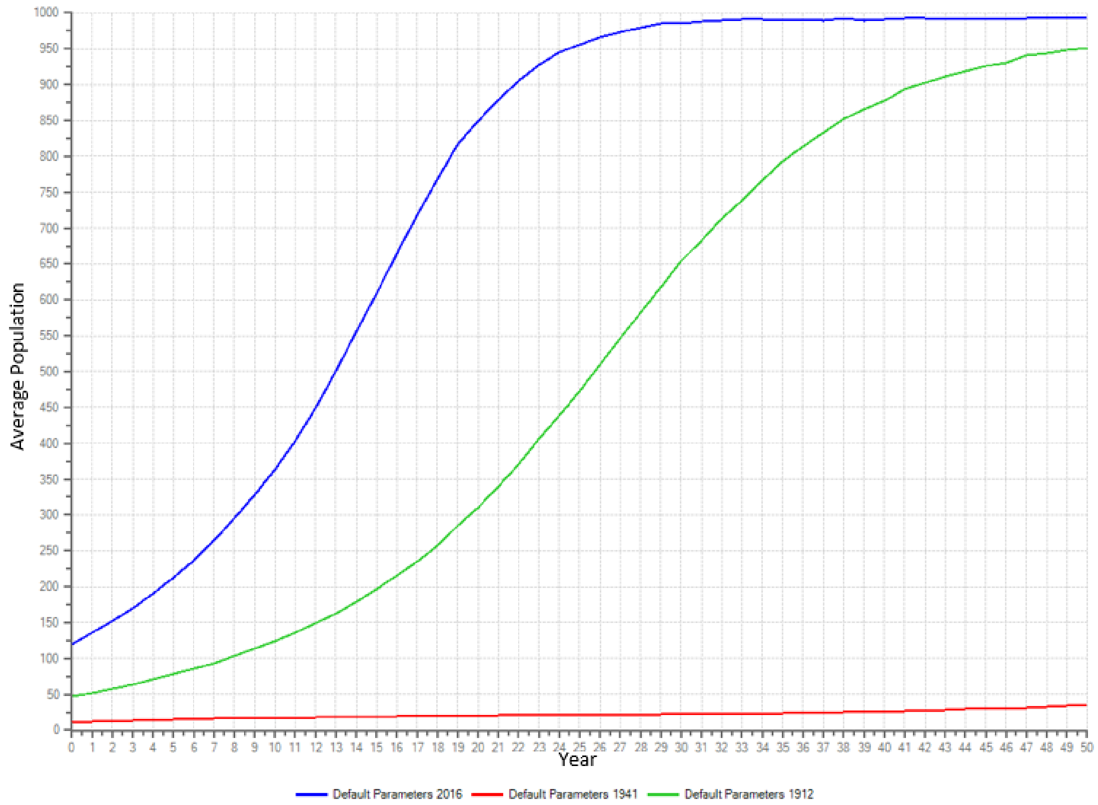


Figure 13. Population Viability Analysis (PVA) of the 1912, 1941 and 2016 peregrine falcon populations from southern England (Sussex) using the default parameters shown in Table 1. The graph plots the average number of individuals from 1000 iterations against the number of years past from the beginning of the simulation (50-year model) starting with the recorded number of individuals for 1912, 1941 and 2016.

The same population groups, 1912, 1941 and 2016, simulated under the same conditions, but with the percentage of females breeding set to 0% to simulate the complete lack of productivity, showed a very different 50-year population scenario resulting in extinction in all cases (Fig. 14). The fastest extinction event was predicted in the 1941 population. The PVA for the 1912 population indicated the probability of extinction was 1.000, with an r= -2.198 and an SD(r) = 0.176. By the 50th year of the 1912 simulation, all populations ended in extinction, with the average number of years to extinction being 13.51. The PVA for the 1941 population indicated the probability of extinction was 1.000, with an r = -2.010 and an SD(r) = 0.226. By the 50th year of the simulation, all populations ended in extinction, with the average number of years to extinction being 7.5. The PVA for the 2016 population indicated the probability of extinction was also 1.000, with an r = -0.226 and an SD(r) = 0.155 . By the 50th year of the simulation, all populations ended in extinction, with the average number of years to extinction being 17.11.

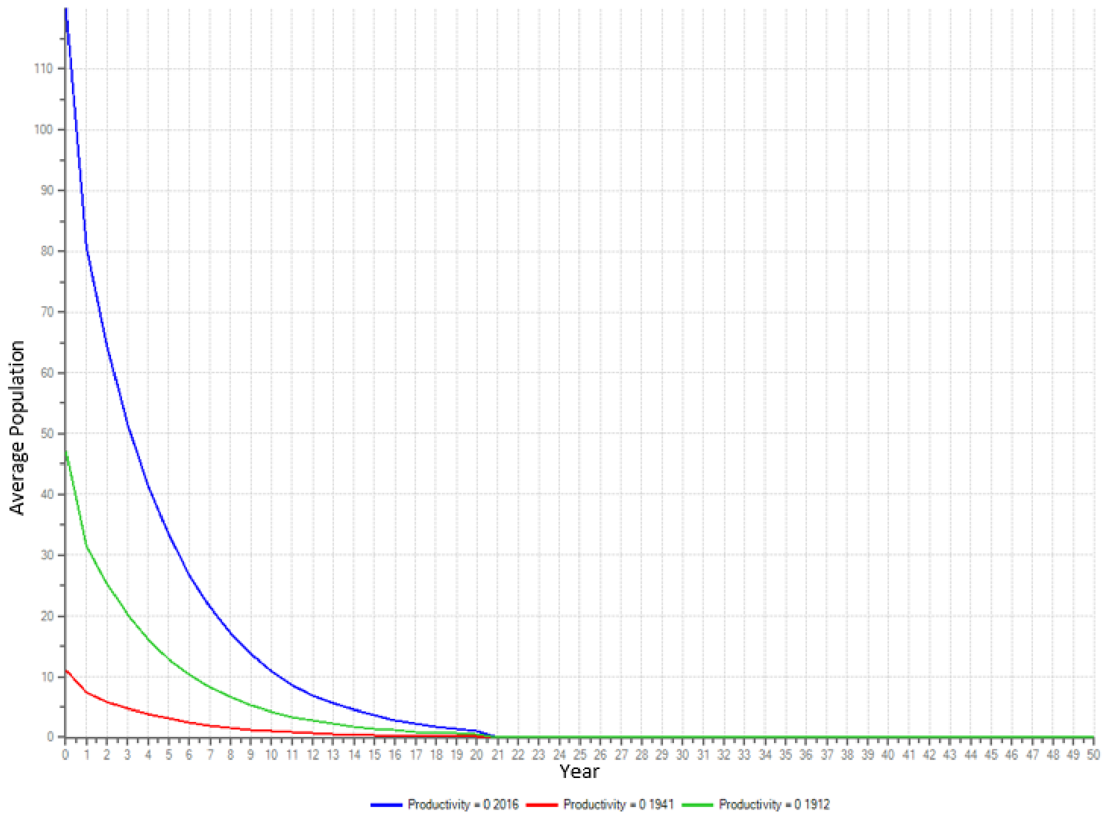


Figure 14. Population Viability Analysis of the 1912, 1941 and 2016 peregrine falcon populations from Sussex using the default parameters shown in Table 1, but with the percentage of females breeding set to 0% to simulate the complete lack of productivity. The graph plots the average number of individuals from 1000 iterations against the number of years past from the beginning

of the simulation (50-year model) starting with the recorded number of individuals for 1912, 1941 and 2016.

Harvest did not have the same impact in the 1912, 1941 and 2016 populations. The PVA with a yearly persecution of 1 male and 1 female indicated that the 1912 and 2016 populations would survive, while the 1941 population would end with extinction (Fig. 15). The PVA for the 1912 population indicated the probability of extinction was 0.163, with an r = 0.048, an SD(r) = 0.141, and a mean time to go extinct of 29.05 years. By the 50th year of the simulation, the mean number of individuals, both extant and extinct, in this population was 629.79, showing an increase of 1340% from the initial population of 47 individuals. The PVA for the 1941 population indicated the probability of extinction was 1.000, with an r = -0.252 and an SD(r) = 0.312. By the 50th year of the simulation, all simulations ended in extinction, with the average number of years to extinction being 4.65. The PVA for the 2016 population indicated the probability of extinction was 0.000, with an r = 0.097 and an SD(r) = 0.117 . By the 50th year of the simulation, the mean number of individuals in this population was 991.05, showing an increase of 826%, from the initial population of 120.

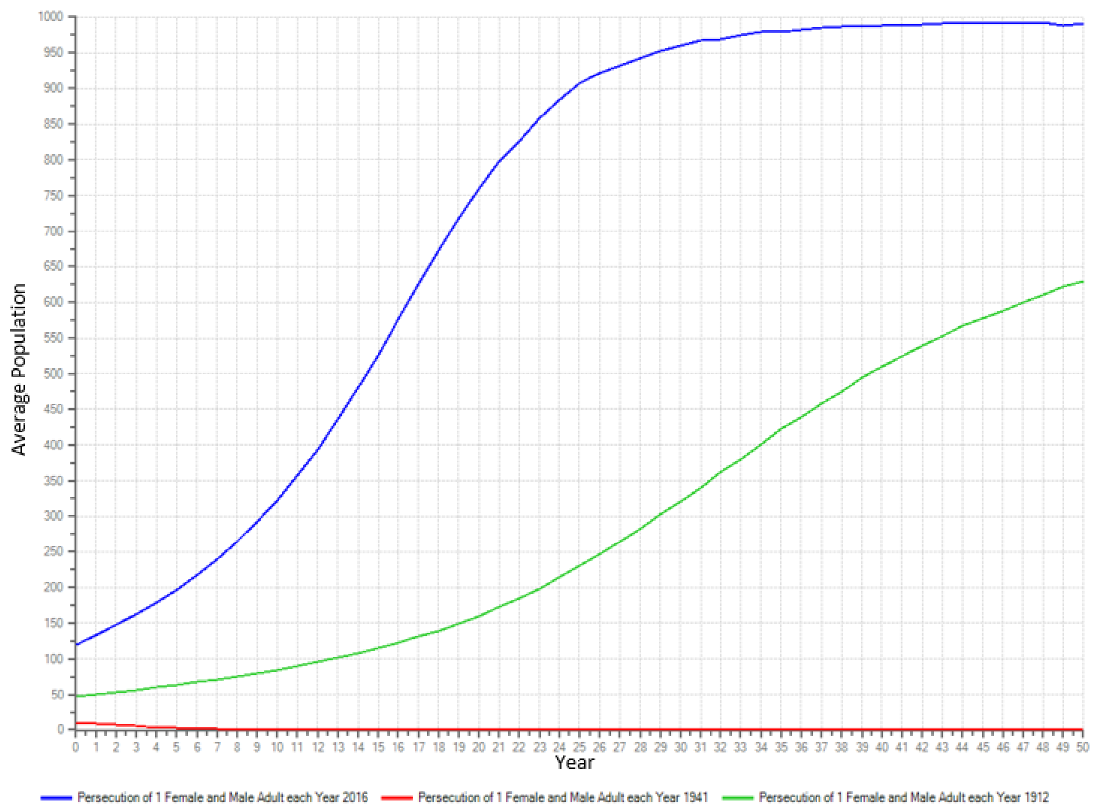


Figure 15. Population Viability Analysis of the 1912, 1941 and 2016 peregrine falcon populations from Sussexusing the default parameters shown in Table 1, but with a harvest of 1 male and 1 female each year to simulate persecution. The graph plots the average number of individuals from 1000 iterations against the number of years past from the beginning of the simulation (50-year model) starting with the recorded number of individuals for 1912, 1941 and 2016.

Under a scenario when there is persecution (in this case set at 1 male and 1 female per year) and intensive egg collection (productivity set to 0), as that seen between 1920-1945, the peregrine falcon populations would have fared much worse than in other models, and even a recovered population like the one in 2016 would go extinct in a few years (Fig. 16). The PVA for the 1912 population indicated the probability of extinction was 1.000, with an r = -0.435 and an SD(r) = 0.191. By the 50th year of the simulation, all simulated populations ended in extinction, with the average number of years to extinction being 6.49. The PVA for the 1941 population indicated the probability of extinction was 1.000, with an r = -0.693 and an SD(r) = 0.274. By the 50th year of the simulation, all simulated populations ended in extinction, with the average number of years to extinction being 2.49. The PVA for the 2016 population indicated the probability of extinction was 1.000, with an r = -0.364 and an SD(r) = 0.169 . By the 50th year of the simulation, all simulated populations ended in extinction, with the average number of years to extinction being 9.92.

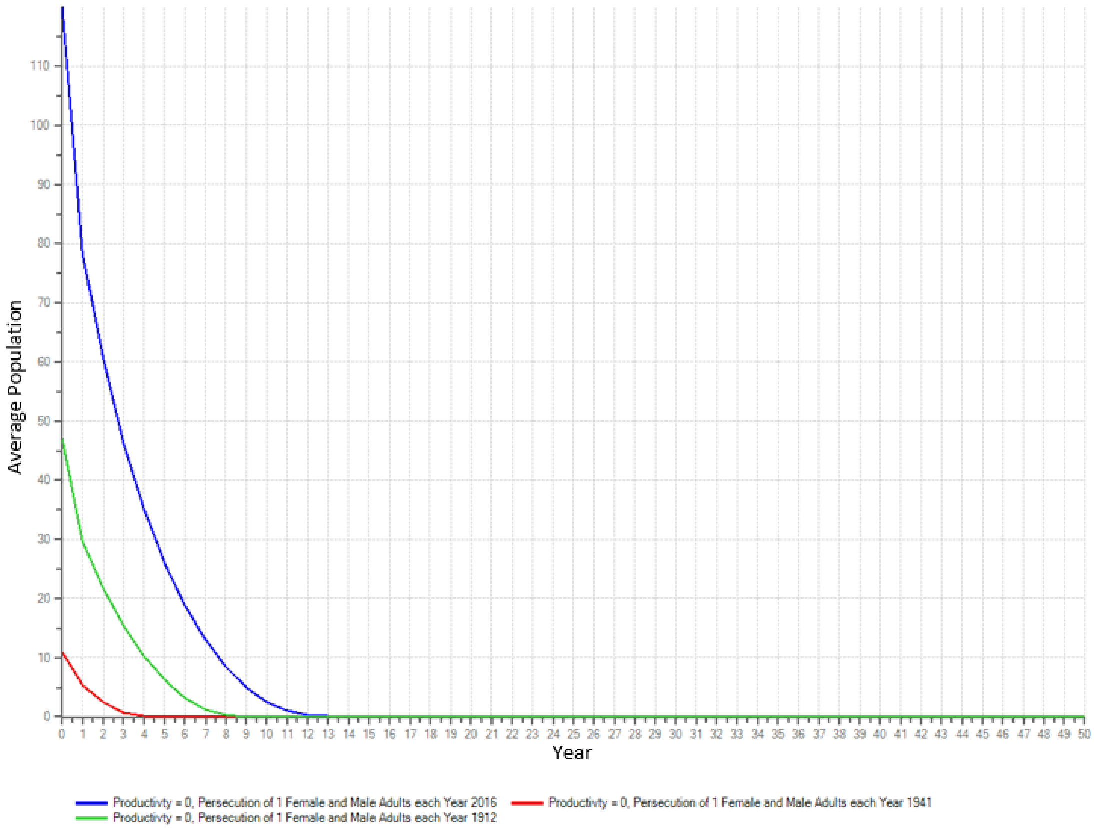


Figure 16. Population Viability Analysis of the 1912, 1941 and 2016 peregrine falcon populations from Sussexusing the default parameters shown in Table 1, but with the percentage of females breeding set to 0% to simulate the complete lack of productivity and a harvest of 1 male and 1 female each year to simulate persecution, which in combination simulate the conditions witnessed during the real population crash of Sussex. The graph plots the average number of individuals from 1000 iterations against the number of years past from the beginning of the simulation (50 years model) staring with the recorded number of individuals for 1912, 1941 and 2016.

The addition of peregrine falcons to the Sussex population through immigrating birds led to a greater mean population growth rate (r) than the default parameters, and caused all models to have a probability of extinction of zero. The PVA for the 1912 population indicated the probability of extinction was 0.000, with an r = 0.0991 and an SD(r) = 0.119. By the 50^{th} year of the simulation, the mean number of individuals, both extant and extinct, in this population was 987.59, showing an increase of 2101% from the initial population of 47 individuals. The PVA for the 1941 population indicated the probability of extinction was 0.000, with an r = 0.094 and an SD(r) = 0.135. By the 50^{th} year of the simulation, the mean number of individuals, both extant and extinct, in this population was 850.21, showing an increase of 7729% from the initial population of 11 individuals. The PVA for the 2016 population indicated the probability of extinction was 0.000, with an r = 1.070 and an SD(r) = 0.116 . By the 50^{th} year of the simulation, the mean number of individuals in this population was 992.77, showing an increase of 827%, from the initial population of 120.

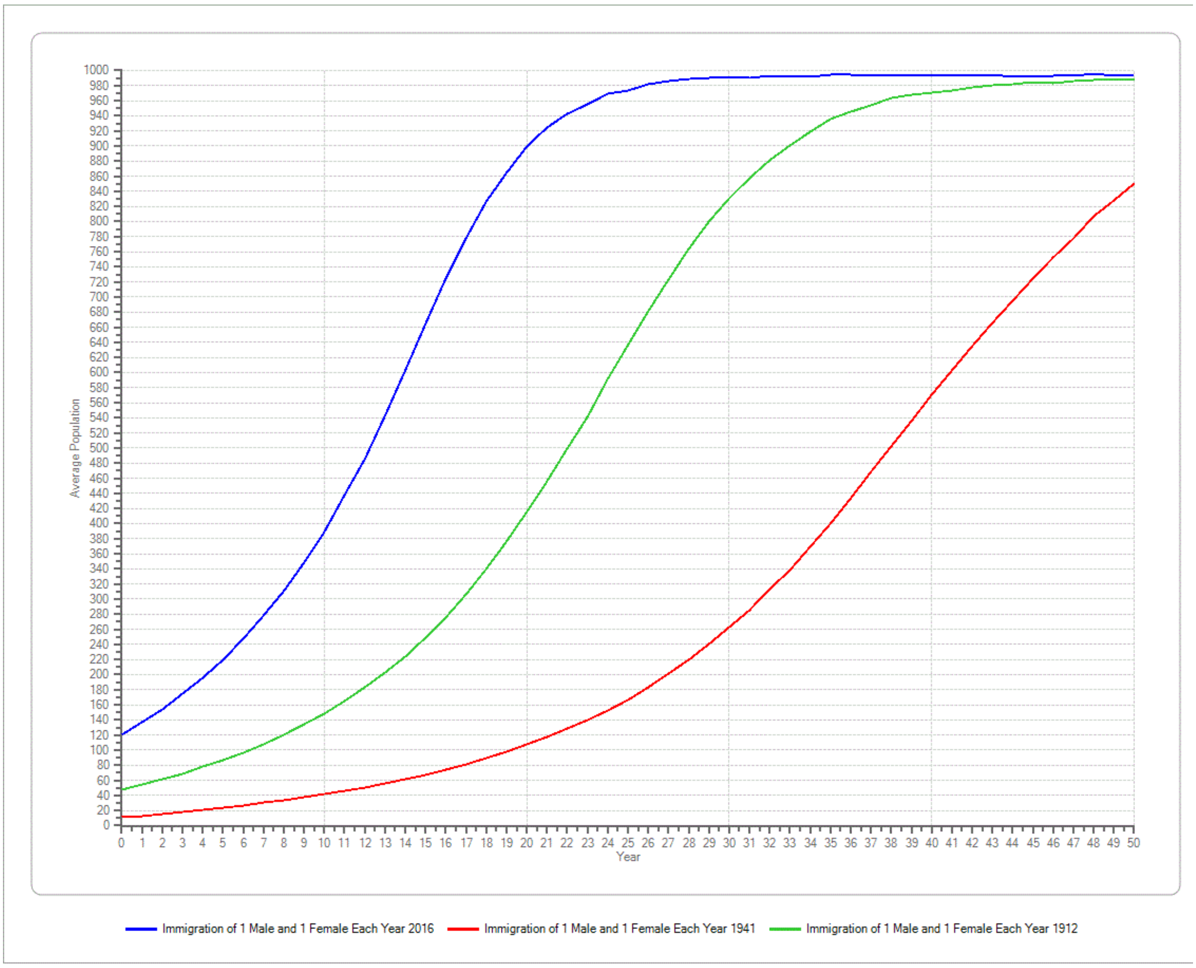


Figure 17. Population Viability Analysis of the 1912, 1941 and 2016 peregrine falcon populations from southern England (Sussex) using the default parameters shown in Table 1, but with the supplementation of 1 male and 1 female yearly to simulate immigration of peregrine falcons into Sussex. The graph plots the average number of individuals from 1000 iterations against the number of years past from the beginning of the simulation (50 years model) staring with the recorded number of individuals for 1912, 1941 and 2016.

Discussion

This study shows the function of using both population modelling and GIS to study threatened populations, using historical and modern data, to gain an understanding of the factors leading to a population collapse, alongside showing how natural recolonisation could take place with only indirect conservation measures being implemented. This is the case of the Sussex peregrine falcon population which, from commonly occurring in southern England, was extirpated by the mid-1950s only to naturally recolonise the area in the early 1990s after some protection measures for wildlife were put into place.

Population viability analyses have been used within raptor studies to determine the probability of survival of a species, whether a population requires supplementation, or to make evidence-based decisions on the number of individuals required to initiate a successful reintroduction of species (Sansom et al., 2016; Schaub et al., 2009). A study conducted on Bonelli's Eagle (*Aquila fasciata*) in Europe used PVA to determine that the population could be at risk of a decline in the next 50 years, and it was determined that the primary conservation concern would be increasing pre-adult survival to have the greatest impact on population, allowing for conservation measures focused on this to be hypothesised (Hernandez-Matias et al., 2013). Their usage of PVA aligns with the focus of this study, which indicated that primary cause of population collapse of peregrine falcons was the lack of productivity. This serves as evidence to support conservation measures that prevent egg collection and removal of nests as a first instance, followed by the protection of adults. The present study further explored the usage of PVA by applying them to extinct populations to gain a better understanding of the population dynamics through a species history; however, this was only attainable due to the extensive records kept by the SPS which date back to 1904 – a unique dataset.

GIS has been used to study habitat selection, monitoring breeding populations and breeding behaviour of raptors (Schmutz, 1989; Wegrzyn and Leniowski, 2011). This can be beneficial in the study of threatened species, as it allows key factors of raptor reintroduction or recolonisation success to be identified, and thus those aspects can be recreated to increase their chance of survival (Jones, 2001). For example, studies on breeding behaviour and nesting preferences of four different raptor species highlighted the importance of habitat selection for species conservation (Withaningsih et al., 2017). The Javan Hawk Eagle (*Nisaetus bartelsi*), the Changeable Hawk-eagle (*Nisaetus cirrhatus*), the Crested Serpent Eagle (*Spilornis cheela*) and the Indian Black Eagle (*Ictinaetus malaiensis*) showed different nest site selection among species and this impacted breeding behaviour and resulted in different times of breeding period in the same landscape (Withaningsih et al., 2017). For *N. cirrhatus*, notable nest characteristics recorded were height, tree species, branch strength and structure, and nest visibility; all which provided a benefit to the survival of the young. While that study hypothesised the primary drivers in nest site selection, for the peregrine falcons recolonising Sussex other factors such as prey availability, nest coverage from weather, the distance of other peregrine falcon nests and the availability of nest sites may be of importance. This demonstrates that peregrine falcons are also versatile as they will use coastal cliffs and a range of other nest sites, including nesting on the ground.

In this study, GIS has been applied to create heatmaps revealing the locations with the highest presence of nesting peregrines, and to document the recolonisation of Sussex since the early 1990s, indicating factors such as the period of nest establishment and the nest type. Through this analysis, the key locations in Sussex to protect to ensure the survival of the majority of current population, alongside the preferred nesting types of the peregrines of Sussex have been identified. Sussex peregrine falcons prefer coastal (cliff) sites, but are now using inland and manufactured sites, presumably due to lack of availability of coastal sites. This indicated that to protect a growing population of peregrine falcons, coastal sites (or cliffs) are important, but that the species would still be able to survive if alternative sites such as quarries and nest boxes in high structures are available. This nest type distribution for peregrine falcons was previously discussed (Ratcliffe, 1963). It has been stated that steep rock faces are essential for breeding to take place, with the majority of these locations found along the coast, and a few inland rock faces. It was also noted that nests are only occasionally placed on the ground or on top of buildings. Due to these preferences, it was stated that the peregrine population of England is greatly restricted in number and geographic distribution (Ratcliffe, 1963). In contrast to this, in modern Sussex, there are more manufactured and inland nesting sites than coastal sites. The modern peregrine population also greatly exceeds both population size and distribution in comparison with that of the 20th century, which was thought to be restricted due to their preference. The reason for this discrepancy is thought to be due to the varying populations of each period (Probst and Weinrich, 1993). The modern population of peregrine falcons in the UK has a far greater number of individuals than that of 1963, which in turn has lead to the peregrine falcons establishing nests in less favoured locations, such as on top of buildings or on the ground (Schmutz, 1989).The expansion of territory following growth in active nesting sites can be seen in Table.2 in which 1954 had 4 nests with a range of 15.0km, 1995 had 9 nests with a range 97.5km and 2016 had 54 active nests with a range of 114.3. In 1995, the entirety of Sussex was covered by the documented peregrine falcons nesting territory, which could indicate why the range growth was much lower proportionally to the difference between 1954 and 1995 (Fig.1). The transition between nest types as Sussex became more saturated can be seen in Figure 6. in which a transition from initial coastal nest up-take, to inland nest up-take and then manufactured nest up-take can be witnessed.

Based on historical records collected by SPS, the peak population size of peregrine falcons, pre-crash, was identified in the year 1912, years before the use of organochlorine pesticides, intense persecution, egg collection and other anthropogenic activities that could have threatened their habitat. The number of active nesting in this year is the greatest prior to crash, at 12 sites with a range of 47.15 kilometres reaching from Hastings to Brighton, indicating how densely populated this area of Sussex was. It can be assumed that the conditions within this region, such as prey abundance or nest suitability, must have been optimal (Selas, 1997; Sergio et al., 2004), with cliff-faces providing optimal nesting sites, alongside the presence of their prey, the rock and feral pigeons (Drewitt and Dixon, 2008; Poirazidis et al., 2007). Productivity, however, calculated as an average of number of eggs, which hatch,divided by number of active nesting sites, peaked in 1917. A study on the Sparrowhawks of Eastern England documented similar findings in population and productivity trends over time

(Newton, 2010), as what can be seen in the peregrine falcons of Sussex, indicating that many raptor populations could maintain, or grow their populations prior to the large influx of anthropogenic disturbances. This also indicates the organochlorine pesticide crisis greatly affected many raptors of the time. This theory is supported by the PVA shown in Figure 7. which shows that under default condintions (lack of anthropogenic disturbances) both the 1912 and 2016 populations continued to grow with percent increases of 2023% and 827% respectivly.

Prior to 1954, when the Protection of birds act was introduced, there were no legal repercussions for killing peregrine falcons or destroying their nests or eggs. This allowed people with prejudice towards raptors to exterminate them with no legal consequences (Newton, 2021). Although in the 19th and early 20th century sport shooting was common, the biggest factor affecting the peregrine falcons in Sussex (and elsewhere in Britain) at this time was egg collecting (Walpole, Reed-Warbler and Partridge, 1939). In the UK, many raptor populations, from different families, have undergone rigorous persecution such as the golden eagle (*Aquila chrysaetos*), hen harrier (*Circus cyaneus*), red kite (*Milvus milvus*), common buzzard (*Buteo buteo*), goshawk (*Accipiter gentilis*) and hobby (*Falco subbuteo*) (Taylor, 2010). For many of these species, their persecution greatly increased alongside the increased popularity and use of reliable firearms, which brought about the sport of shooting (Price and Robinson, 2008). When examining the impact of persecution on the 1912 historical population, it can be seen that by just removing 1 male and 1 female from the pool annualy, the growth rate becomes 0.048, just over half of the 0.085 observed in the default PVA model (Fig.7; Fig.15). The probabilty of extinction also grew from 0.000 in the default PVA to 0.163 in the persecution model, showing how the removal of just two individuals annulay could potentially lead to the collapse of a population.

How could the peregrine falcon have avoided extinction during intense egg collection and persecution? What must be noted about this period is that, despite sport shooting and extensive egg collection in the cliffs of Sussex, particularly by Walpole-Bond during 1904-1921, and only a few young birds being produced, the adult population still survived. This is most likely due to immigration from surrounding populations of peregrine falcons which underwent less egg harvesting, or because some adults nested in non-coastal sites (as has been observed in the post-crash population). To test the impact of immigration, a PVA was created in which 1 male and 1 female were added to the population annually (Fig.17). Under these conditions all three populations had a 0.000 probability of extinction, marking a reduction of 0.626 for 1941 under default conditions (Fig.13). This not only indicates to the value of imiigration on the survvival of threatened populations, but also the impact of immigration on bolstering smaller populations. Also, throughout 1904-1921, Walpole-Bond did not take every egg, often opting not to raid some specific nest such as Beltout and the Western Seven Sisters. Other nests such as both Beachy head West and East, appeared to be difficult to access, as no eggs were taken from these until 1943, even throughout a peak period in egg collection. A second potential explanation for the survival of this population during early 20th century is due to the peregrine falcon's ability to lay a second clutch of eggs if the first one is lost in the early stages of incubation (Burnham, Sandfort and Belthoff, 2003). In this scenario, an alternative nesting site is commonly used, which would have allowed the birds to successfully rear a second clutch (Burnham et al., 1978). This behaviour can also be witnessed in other raptor species, such as the lesser kestrel (*Falco naumanni*) or the sharp-shinned hawk (*Accipiter striatus*) (Catry et al., 2016; Delannoy and Cruz, 1988).

The PVA provided evidence that the populations in 1912 could have avoided extinction even if the conditions of population harvest would have prevailed, and that the population would have continued to grow. Due to the impact of egg collection on young production, there was a trend in which the number of young did not greatly exceed the number of nests, despite peregrine falcons having an average brood size of 3.28 (Robinson, 2005). If the eggs were not being removed from the nests, it would have been expected to see around 24 young produced yearly on average, calculated by multiplying average nest size by the average untainted number of offspring. When searching for literature pertaining to conducting a PVA on a historical population of a species, two conflicting studies were found, the first one (Brook et al., 1997) warning of the inaccuracies of PVA and the second one

(Brook et al., 2000) praising the accuracy of PVA. The first study concluded that when using PVA, many different simulation packages should be tested as some default parameters may be inaccurate or untested, and to ideally use packages that have been retroactively tested (Brook et al., 1997). It was stated, however, that many of the parameters relating to the test species were unknown at the time, particularly the carrying capacity (K). In the present study on peregrine falcons, the majority of parameters were known due to the extensive records kept by Walpole-Bond and the SPS, which should in turn provide accurate results. In contrast to the first study, the second one analysed the accuracy of 21 long-term ecological studies by conducting retroactive PVAs on each of the products (Brook et al., 2000) and found the predicted models and reality to be very similar, with the population sizes being close to one another. They concluded that PVA is an accurate tool in the management of threatened species. As this study conducted on the Sussex peregrine population used a majority of known parameters, it would be more akin to this latter study, inferring the model should be quite accurate to the real-world population.

The year 1950a marked the beginning of the population crash for the UK peregrine falcons (Ratcliffe, 1984). If the peregrine falcon population would not have undergone a continuous decline in number of individuals, the 1941 population would have been expected to grow, based on modelling results, and slowly occupy the remaining area of Sussex. The increasing number of peregrine falcons would have to use less ideal, but available, alternative nesting sites such as in-land quarries and manufactured structures (Probst and Weinrich, 1993; Schmutz, 1989), but would have still been able to reproduce. In 1941, the Sussex government released a license to destroy peregrine falcons in their county, this lead to Walpole-Bond beginning to shoot them (Sussex Peregrine Study, n.d.; Taylor, 2010). In 1946, peregrine falcon activity was seen at 8 nesting sites, with 4 confirmed to be occupied by pairs. The territory for these falcons covered the same range as seen in the previous phase; however, two nesting sites were lost around Seaford due to cliff collapse, and one new one was established. In a study on the peregrine falcons of Britain (Ratcliffe, 1981), it was seen that from 1930 to 1962 there was an average 33% decline in nest occupation, with southern regions suffering from higher rates of decline than northern regions. Organochlorine pesticides were also widely adopted during the 1940s (Dunlap, 2014) causing egg mortality due to egg thinning as they would be accidentally destroyed by the parents during incubation (Holm et al., 2006). After this post-war period many populations of raptors were seen plummeting, primarily due to the usage of organochlorine pesticides. Kestrel and sparrowhawk populations declined between 1963-1992 and continued to decline even more sharply from 1992 to 1997 (Newton, Wylie and Dale, 1999), by which time the peregrine falcon in Sussex was already recovering. The population trends of kestrels and sparrowhawks highlight the impact of organochlorines in the health of many raptor populations. The geographical distribution of peregrine falcons also helped in their recolonisation and possibly resulted in the genetic similarity of pre- and post-crash peregrine falcon populations in Britain (Weaving et al., 2021).

From 1912 up until 1953, the number of active nesting sites of peregrine falcons fell to just 1 observation, a clear downward trend as the years progressed. It was noted that from 1952 no young were produced (productivity = 0) due to the fact that no successful eggs were being laid by the parents (Kolaja, 1977). By 1953 no active nesting sites were witnessed again, apart from a single nest occupation recorded in 1963 (which could have been an error in the records, or a failed attempt for reproduction). This year was the culmination of multiple factors leading to the inability of peregrine falcons in Sussex to produce viable offspring. Over this period, the legislation toward raptor persecution was relatively lax (Brown, 1997). The reason active nests were reported until 1952 would likely be due to the few local survivors and immigration from nearby regions who would use the nests sites available (Jackson and Sax, 2010). This would also explain how the number of active nesting sites would increase, despite there being 0 young produced (Krauss, Steffan-Dewenter and Tscharntke, 2003). The final factor leading to the population crash and extirpation of the Sussex population was the widespread adoption of organochlorine pesticides in the post-war era, which drastically reduced the number of young being produced due to egg-shell thinning causing failure at the incubation stage (Ruus et al., 2010; Blus, 2011). While both egg collecting and persecution greatly impacted the population, the impact of pesticides alone greatly outweighed both of these factors (Bednarz, 1989). The low productivity was unsustainable and ultimately lead to the population collapse. This was evidenced by the use of PVA with harvest and egg mortality, showing that even the recovered (and numerous) population of 2016 would collapse quickly. With the advent of technological and agricultural developments, and a combination of intense persecution, fashionable egg collecting activities, and environmental pollution, the population of peregrine falcons in Sussex finally collapsed.

It was not until 1989 when peregrine falcons were observed again nesting on the southern cliffs of Sussex, with the first offspring being produced in 1990 (Sussex Peregrine Study, n.d.). Despite the lack of active nesting sites within Sussex between 1953 and 1989, peregrine falcons were still seen around, but no active nesting was observed nor recorded. From 1989, the number of active nests grew rapidly, and by 2016 there were 35 observed nests and the highest number of peregrine falcons on record. The pre-crash population had the highest number of eggs laid in a year; however, the number of eggs laid was only recorded by SPS until 2003. Although number of eggs laid in the post-crash phase did not appear to be as high as in the pre-crash phase, it is reasonable to assume that a minimum of 50 would have been laid in 2016, indicated by the number of young produced, which far exceeded pre-crash records as early as 2003. A growing population indicates that during this period the population was healthy and could continue to expand if no intervention was undertaken (Sibly and Hone, 2002); this was also evidenced by the PVA showing that all populations (1912, 1941 and 2016) would have increased in size and avoided extinction.

Leading up to this period in time, many conservation efforts were put in place to prevent the complete extinction of the peregrine falcon in the UK, this includes a complete ban against killing peregrine falcons, a ban against taking their eggs or destroying their nests and the ban on using many organochlorine pesticides, including DDT, aldrin, dieldrin and endrin (Crick and Ratcliffe, 1995; Fisher and Walker, 2016; Fletcher et al., 1999; Morris, 2019; Wildlife and Countryside Act, 1981). The changes in legislation and conservation practices in the UK ensured that the number of active nesting sites and successful breedings would potentially increase, unless birds, chicks or eggs died of natural causes (Newton et al.,1986; Smith et al., 2015). The productivity witnessed during the post-crash was assisted through the availability of nesting sites and the introduction of laws to protect wildlife (Jones, 2001; Woodroffe, Thirgood and Rainowitz, 2005). These changes were helpful in the conservation of the species (Blus and Henry, 1997; Sergio, 2001); however, some are still ignored by some members of the public so a small amount of harvest can still be expected to occur (Burnside, Pamment and Collins, 2021). Moreover, the true value of this conservation measures to peregrine falcons in the UK has not yet been fully evaluated (Parrott, 2012; Sears and Avery, 1993). With the ban of organochlorine pesticides, the protection of adults, and availability of manufactured structures, the peregrine falcons were successfully able to produce young once again and survive, allowing for new generations to inhabit new nesting sites and further increase the number of young being produced (Smith et al., 2015). What must be noted about the conservation measures which assisted in the recovery of the peregrine falcon in the United Kingdom, is that they were blanket legislation which covered the peregrine falcon, as opposed to direct legislation brought in specifically for the conservation of peregrine falcons. In the UK, the recovery of the peregrines was also unassisted, meaning it provides the opportunity to study the natural recovery of a previously locally extinct species. This is unlike many other countries such as USA and Germany for example, who released captive-bred peregrine falcons into the wild to bolster the population (Saar, 1985; Vera et al., 1997). Successful recoveries have been witnessed in both the UK's unassisted population and in the many assisted populations globally, with no genetic bottlenecking witnessed in either group. This provides validity to both of the methods used, however this raises the question of the origins of the UK peregrine population and allows for a study on unassisted natural recolonisations to be conducted.

When recolonising Sussex, the initial peregrine falcon population had access to the historical nesting sites, which were quickly used and all re-established by 2003 (Weaving et al., 2021). The density of active nesting sites in Sussex during this period was relatively high due to the ideal ancestral nesting site for peregrine falcons in Sussex being coastal cliff sites (Franklin and Everitt, 2009). Coastal sites are ideal locations for peregrine falcons as they provide good shelter from the weather, high altitude for hunting and good prey availability (Brambilla, Rubolini and Guidali, 2006; Wightman, 2005). Coastal sites are also considered ancestral to the peregrine falcon so the use of this nest type could be an instinctual drive (Houle, 1999). As over 40 years had passed since the collapse and recolonisation of the Sussex population, there were now also new manufactured sites which were optimal as nesting sites. Examples of this would be Fitzleet house built in 1960, or the Amex Stadium constructed in 2008 (emporis.com, 2022; greatbritishlife.co.uk, 2021). Through the chronological records of the use of coastal, inland and manufactured nesting sites, nest preference over the recolonisation period can be observed, with the prefered nest type being established first, and the least favoured nest type being left until last (Pampush, 1980). As the number of available nest sites are decreasing due to an increased population, the falcons begin occupying less suitable sites (Doyle and Wright, 1998). Moreover, cliffside erosion can also create or remove suitable nesting areas as new scrapes are formed (Blanco, 1998).

In the early time of recolonisation, a bias towards nest establishment in south-western Sussex was observed, which could be used as an indicator of the initial population coming from further west, presumably in Hampshire, and suggested that the falcons were following the coastline. Initial coastline colonisation would be expected, as they are the favoured nest type of the peregrine falcon (Ratcliffe, 1963). Later on, as the most optimal coastal nesting sites were taken, peregrines established inland nests, and then moved on to manufactured structures. This transition further reinforces the idea that inland nesting sites are preferred over manufactured nests. Inland sites provide locations with less human presence or disturbance and can also offer weather protection alongside prey availability; however, some of these locations do not provide optimal coverage, leading inclement weather to cause juvenile mortality (Mearns and Newton, 1984; Vera et al., 1997).

As the coastal sites were taken, the falcons moved northward and eastward, and manufactured nesting sites are now the most widely used sites by peregrine falcons as the majority of traditional nesting sites have already been occupied (White, Pruett-Jones and Emison, 1980). This result was witnessed with an initial up-take of coastal nesting sites, followed by inland nesting sites and then manufactured nesting sites (Fig.1; Fig.5). However, another possibility for a shift from coastal sites could be cliffside erosion which ultimately changes the cliff face (Blanco, 1998). In the latest recolonisation period, the newly established nesting sites are documented in the east, signifying the saturation of their preferred location in the west. Inland quarries, defined as nesting sites not within a coastal area and lack the presence of manufactured structures such as nesting boxes or buildings, have been used since the initial recolonisation phase. This nest type was first established in 1992 and continued to have new nests established, a record of 25 years. Some inland nesting sites can also be old raven nests within trees and cliffs, or in some cases just nests created on the ground (Jon Franklin, SPS member, pers. comm). With this relaxed disposition in selecting nesting locations, peregrine falcons in Sussex could colonise a wider area. manufactured nesting sites can be highly variable in suitability, with some speciality nest boxes providing perfect conditions for the birds, while others are wholly unsuitable such as gutters on a block of flats (Gahbauer et al., 2015; Dwyer, Hindmarch and Kratz, 2018). Due to the presence of humans, prey availability is most likely high around these nests; however, this also comes alongside human disturbance which could scare off nesting peregrines and increase their stress levels, ultimately reducing fitness (Bird, Varland and Negro, 1996; Cade, Martell and Redig, 1996).

The PVA results for the modern parameters showed that any robust population of peregrine falcons in Sussex would be able to survive and grow under modern conditions. Due to the lack of anthropogenic disturbances in this period, thanks to introduced legislation, a healthy population can grow, with the rate of growth being determined by the initial population size. Even under these optimal conditions, 1941 still had a probability of extinction greater than half. This infers that the peregrine population in 1941 was too depleted at this stage, due to the anthropogenic factors, to recover even under the best conditions. In a study conducted on the possible reintroduction of peregrine falcons in the USA, the results indicated that the conservation measures already introduced were effective enough to create a growing population, without the need for the release of more captive birds (Wakamiya and Roy, 2009). Similar to the recolonisation of Sussex, it was witnessed that the current peregrine falcon population in the USA, alongside the measures in place, were sufficient to create a self-sustaining population; however, this was achieved naturally in the UK, while the US was recolonised through a captive breeding and release programme.

When measuring the impact of no productivity through the use of PVA, it is revealed that this factor played a big role in the collapse of the Sussex peregrine population. As expected, once the existing population at the start of the simulation had died out, the simulation would come to an end, as there were no offspring being produced to create population growth. Extinction was the guaranteed result of these tests, however, this model was used to determine the impact of initial population size and robustness on the time taken to reach extinction. In all three populations an extinction probability of 1.000 is seen, indicating that no matter how robust a peregrine population is, they would not be able to survive the productivity values witnessed during the peregrine falcon population collapse, however, the more robust populations have a longer mean time until extinction. The outcome of this model is most likely due to the age distribution of the populations, the larger population are to have more young individuals under the stable age distribution used, and thus have the highest probability of surviving longer in the given conditions. From the records it is known that the Sussex population can continue exclusively through immigration (presumably from neighbouring counties), explaining why the localised extinction of Sussex did not occur during Walpole-Bond's egg collecting period. The impact of immigration could not be accurately simulated in Vortex due to the broad geographic range and distribution of peregrine falcons (resident in the UK and migratory from other countries), making the immigrating population of Sussex unknown. However, when a catastrophe, such as the organochlorine pesticide crisis, prevents all individuals of the species across its range from reproducing, the population can no longer persist as immigration becomes negligible or non-existent.

When examining the impact of persecution from the PVA, it is evident that the more robust populations of peregrines in Sussex can not only survive, but can still grow with the rate of persecution witnessed during its peak period, as seen through the growth of the 2016 and 1912 populations. From this, it can be inferred that any conservation efforts targeting exclusively the killing of adult peregrine falcons would not have prevented the population collapse; instead, the problem of low productivity would need to be tackled. However, by removing the pressure of peregrine falcon persecution, robust populations would be able to grow fast and small populations will likely not become extinct. A study examining the impact that persecution would have on the Griffon vulture (*Gyps fulvus*) population of Croatia, it was revealed that if it continued at its current rate, the population would decline; however, if it stopped entirely, it would only increase the population by 3% yearly (Pavokovic and Susic, 2005). This model was run at a population size of 146. In contrast to this, the PVA analysis conducted here revealed that the impact from persecution was negligible on robust populations and that the population could in fact still continue to grow. This is likely due to peregrine falcons being able to reproduce at the age of 2, while griffon vultures cannot reproduce until they are 5 years old, meaning that the vulture has to survive for longer to be able to successfully reproduce (Duriez, Eliotout and Sarrazin, 2011).

When testing the impact of immigration on a default population of peregrine falcons, using a model in which 1 male and 1 female were added to the population, as expected, all populations rate of growth (r) saw an increase, with the smaller initial population sizes being more greatly affected. The impact observed on the smaller population size provides evidence towards the theory that the 1912 population, despite having minimal successful young reared each year, could still survive and grow exclusively from immigration of peregrine falcons within the wider area. The reason for a higher growth in the smaller populations is attributed to the carrying capacity of Sussex being reached prior to the final year of the simulations run-time, causing the populations growth rate to plateau. However, the volume of immigrating individulas into Sussex, would be minimal during the population crash as there were very few birds in the southeast of England at this time who could immigrate from surrounding counties (Ratcliffe, 1980). This highlights the importance of the conservation measures put in place to tackle the falling productivity, as regardlesss of the effect of immigration on populations in simulations, if there are no individuals who are able to immigrate, the factor will never be present in the real-world populations. The impact of immigration on small populations of long-lived birds determined that immigration not only had a strong impact on the number of breeding pairs in the colony, but also greatly increased the productivty through the addition of breeding adults to the population (Soriano-Redondo et al., 2018). This study highlights the importance of immigrating birds on small populations, indicating the theoretical growth possible on a declining population, such as the historic Sussex population, if there are birds available to immigrate in the wider landscape.

When studying the combined impact of persecution and lack of productivity witnessed during the collapse of the peregrine falcon, it is known that all of the populations, regardless of size would become extinct. In this analysis, the two main contributing factors which formed the localised extinction of the peregrine falcon in Sussex, being persecution and pesticide poisoning, were tested together, and as expected complete extinction still occurs due to the inability to produce young; however, with the added effect of persecution, the mean time until first extinction was reduced significantly. This highlights the importance of tackling the low productivity through conservation measures, while providing insight into the compounding damage caused by persecution. With these factors being tested simultaneously, both the juvenile and mature peregrines are directly affected, leading to the complete collapse of the populations. While persecution alone is enough to destabilise low initial population models, it is indicated that more robust populations can survive this, whereas 0 productivity causes extinction in all populations, indicating the severity of it.

Conclusions

Through examination of the records pertaining to the historic distribution of peregrine falcons in Sussex from the early 1900s, a few conclusions can be reached. The first conclusion is that the population has seen a well-recorded change through time since the 1900s, with a healthy and relatively undisturbed population, followed by a population affected by persecution and egg collection, and a complete collapse primarily due to a combination of these factors. Perhaps the significant factor driving the collapse was the use of organochlorine pesticides. Since the 1990s, an apparently healthy population re-established naturally in southern Sussex, greatly exceeding the population size in the initial records. Conservation, environmental monitoring, changes in agricultural techniques, and human attitudes towards birds of prey have allowed the return of the peregrine falcon, and based on population modelling the future of the Sussex peregrine falcon population appears highly viable if current conditions prevail.

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