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BARN OWL BREEDING IN AGRICULTURAL LANDSCAPES OF GREAT BRITAIN

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Abstract

Habitat loss and fragmentation associated with agricultural intensification have affected farmland biodiversity worldwide. Large tracts of heterogeneous natural habitats are transformed into homogenous agricultural lands thereby resulting in a decline in farmland bird populations. The resultant decline in farmland bird populations can be associated with unsuitable foraging habitats, a decline in prey resources and an increase in chemical pollutants such as pesticides associated with agriculture. In this thesis, I use the widely studied and monitored farmland raptor species, the barn owl (*Tyto alba*) to examine the effects of agricultural landscape composition of different crop types, and the pesticides used in the cultivation of cereal crops, the most dominant crop type in Great Britain, on barn owl brood size (a proxy for barn owl productivity) and nestling body mass (a proxy for nestling body condition). In addition, I also explore the impact of the most dominant crop type, cereal crops, on the diet of the barn owl in Great Britain.

Previous studies on barn owl breeding success in relation to land use in the South Midlands and South East of Great Britain have shown that barn owl breeding is independent of land use. However, these studies are local and use broad habitat types. In this novel study (Chapter 2), the effects of agricultural landscape composition of different crop types on barn owl brood size and nestling body mass across a national level and a regional level between three regions of Great Britain, namely the Midlands, the South East and the South West, with varying degrees of agricultural intensification, are examined. Among all crop types, fruit/forage crops have a positive impact on barn owl brood size, whereas, cereal crops have a negative impact on barn owl productivity, with a greater total area of cereal crops predicting smaller brood sizes. I build on using the landscape composition of cereal crops to further explore the impacts on aspects of barn owl reproduction in Chapter 3, where the effects of the landscape composition of cereal crops on maternal barn owl body condition and consequently the impact on barn owl brood size and nestling body mass is determined. Here I show that the perimeter:area ratio (a proxy for habitat complexity) of cereal crop fields has a positive impact on the maternal body condition of barn owls with a greater perimeter:area ratio of cereal crops predicting larger brood sizes. Building on the results of both Chapter 2 and Chapter 3, the impact of four commonly used pesticides by weight, in the cultivation of cereal crops namely, fungicides (chlorothalonil and diflufenican) and herbicides (glyphosate and flufenacet), on barn owl brood size and nestling body mass is investigated. An increase in the use of the herbicide flufenacet has a negative impact on barn owl brood size in Great Britain. Finally, in Chapter 5, the impact of the landscape composition of cereal crops on the diet of the barn owl in the Midlands and South East, the two regions that showed differential responses in the impact of cereal crops on brood sizes in Chapter 2 and Chapter 4, is determined. The number of prey items recovered in the diet of the barn owl decreased with an increase in the total area of cereal crops.

The findings of this study demonstrate that barn owl reproduction is not influenced by agricultural landscape alone, but by a series of knock-on effects of agricultural landscape composition and management practices on life-history traits such as maternal body condition of breeding barn owls, and on prey availability around barn owl nest boxes. Finally, Chapter 6 offers recommendations to improve the quality of life for barn owls, with implications for the conservation of all farmland species.

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Table 2. 2. Generalised linear mixed models with Conway-Maxwell Poisson distribution and loglambda link function predicting barn owl brood size. Fruit/forage crops and cereal crops were the only models with $\Delta AIC_c < 2$ and are in bold. The intercept corresponds to the Midlands, and individual effects of number of patches, perimeter:area ratio and total area are presented in the row corresponding to the intercept. 95% Confidence intervals are provided within parentheses and significant interactions are in bold. ICC – Intraclass correlation coefficient, R^2 (Cond.) – R^2 Conditional, R^2 (Marg.) – R^2 Marginal.

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Chapter 1

Introduction

Anthropogenic activities such as changes in land use, hunting, and the introduction of invasive species have accelerated biodiversity decline worldwide (Tilman *et al.*, 2017). Among these activities, land-use changes accompanied by habitat loss and fragmentation pose one of the biggest threats to terrestrial mammals and birds (Newbold *et al.*, 2015; Joppa *et al.*, 2016). For example, habitat loss and habitat fragmentation can result in a decrease in the size of natural habitats that a species can occupy thereby affecting their abundance and resulting in fragmented populations (Ceballos and Ehrlich, 2002). Other anthropogenic activities like hunting, for example, have affected nearly 40-50% of threatened terrestrial mammals and birds (Tilman *et al.*, 2017), whereas the introduction of invasive species in some cases has decimated many species of island birds (Blackburn *et al.*, 2004). Among all the anthropogenic-induced threats to biodiversity, nearly 80% of bird species and 75% of mammal species are threatened by the agriculture sector alone (Tilman *et al.*, 2017). Furthermore, future projections suggest that agricultural intensification can reduce the global biodiversity value of agroecosystems by 11% by 2040 compared to 2000 (Egli *et al.*, 2018). Therefore, agriculture-driven habitat loss and habitat fragmentation are constant drivers of global biodiversity loss.

Nearly one-third of global land use is apportioned for anthropogenic activities (Imhoff *et al.*, 2004), and the transformation of natural habitats to suit agricultural needs is one of the major drivers of biodiversity decline (Foley *et al.*, 2005). Agricultural intensification, therefore, results in heterogeneous natural habitats converted to homogenous agricultural lands which can alter ecosystem dynamics (Jongman, 2002; Jeliazkov *et al.*, 2016). For example, land transformation associated with agriculture can result in an increase in intermediate trophic predators such as jays (*Garrulus glandarius*) and a decrease in apex predators such as the goshawk (*Accipiter gentilis*) thereby altering trophic interactions (Andren, 1992). A lack of suitable foraging habitats can result in a decline in the presence of apex predators in agricultural landscapes (Mirski and Väli, 2021). In another study by Dunn et al. (2016), it is shown that microhabitats in agricultural landscapes such as unmanaged hedgerows can further expose species such as songbirds to predators such as corvids. Consequently, the transformation of natural habitats to suit agricultural needs can alter ecosystem dynamics resulting in the decline of farmland species such as farmland raptors, with an increase in habitat generalist species such as corvids (cf. Clavel, Julliard and Devictor, 2011; Devictor; Julliard and Jiguet, 2008).

Among birds, the impact of agriculture is species dependent and a decline in farmland bird populations can either be a result of a lack of food resources, use of chemical agents such as pesticides, grassland management practices, and grazing or a combination of all these factors (Newton, 2004). For example, a decline in seed-eating birds can be a result of the use of herbicides in farming, which can destroy seed-producing weeds that are the primary source of food for seed-eating birds (Newton, 2004). Furthermore, the populations of seed-eating birds can also suffer from grassland management practices, where a reduction in sward height can result in a loss of food resources for seed-eating birds by halting the flowering of seed-producing plants (Vickery *et al*., 2001). Maintaining short swards of grass can also affect seed-eating birds as short swards of grass provide poor camouflage against predators (Vickery *et al*., 2001). As a result, seed-eating birds in agricultural landscapes are affected by both the use of chemical agents such as herbicides and grassland management practices. Among game birds such as the black grouse (*Lyrurus tetrix*), grazing intensity can have a negative impact on reproduction thereby affecting population numbers (Jenkins and Watson, 2001). For example, a study by Baines (1996) showed that the breeding success of the black grouse was 37% lower in heavily grazed fields, suggesting that a lower number of large herbivores could contribute to an increase in the number of insect prey for black grouse thereby facilitating in its sustenance. Similar results were obtained in a study by Smith *et al.* (2001), where the decline of a passerine bird the meadow pipit (*Anthus pratensis*) was associated with overgrazing, which resulted in smaller sward heights associated with a decrease in insect prey abundance and diversity. Therefore, passerines in general are affected by grazing intensity in agricultural landscapes. Despite the minor differences in the causes of the decline of passerines and gamebirds, the predominant factor uniting the decline in farmland birds is the lack of food resources because of agricultural practices.

While agriculture directly impacts farmland birds that comprise intermediate trophic levels, the impact of agriculture on higher trophic levels such as raptors is more pronounced (Duffy *et al*., 2007). This is because it is energetically demanding to sustain apex predators such as raptors, as they feed on intermediate or lower trophic level species, and consequently the conversion rate of biomass across the different trophic levels is slow (Duffy, 2003; Duffy *et al*., 2007). Thus, raptors are often considered reliable indicators of ecosystem health (Sergio *et al*., 2008). Of all bird species, the raptors are more threatened than other birds with 18% of worldwide raptor species threatened with extinction, while 52% of raptor species are known to have declining populations (McClure *et al.*, 2018). Agriculture poses the biggest threat to raptors compared to other anthropogenic threats such as logging, hunting, fishing, fires and pollution (McClure *et al*., 2018). From the viewpoint of conservation of farmland biodiversity, raptors can act as a conservation flagship as they are reliant on species of intermediate and lower trophic levels for their continued sustenance in farmland ecosystems (Donázar *et al.*, 2016). Therefore, studying the impacts of agriculture on the life-history strategies of farmland raptors such as reproduction can contribute to the greater good of farmland biodiversity conservation.

1.1 Role of raptors in ecosystem functioning

1.1.1 Biological pest control

Agricultural intensification involves the transformation of heterogeneous natural habitats into homogenous agricultural lands (Dudley and Alexander, 2017). The converted homogenous agricultural lands can be free of all predators, pathogens, and parasites, and can result in a breeding ground with plenty of food for several anthropophilic species such as rodents (Donázar *et al.*, 2016). Historically, chemical agents such as anticoagulant rodenticides were used to combat rodent breeding and protect crop output (Hadler and Buckle, 1992). At present, secondary exposure of anticoagulant rodenticides to raptors has resulted in a decline in raptor numbers due to severe blood loss and internal haemorrhaging (Gomez, Hindmarch and Smith, 2022). Reassessments of the negative impact of the use of anticoagulant rodenticides on raptors contributed to the proposition of including different methods to tackle rodent pests, including biological control by raptors (Bianchi, Booij and Tscharntke, 2006; Donázar *et al.*, 2016). In the 1990s, Integrated Pest Management (IPM) scheme began to create interest as an alternative to the use of rodenticides to control rodent populations in agricultural landscapes (Donázar *et al.*, 2016). The IPM scheme aims at using biological and cultural methods to tackle rodent populations by limiting the use of chemical agents such as rodenticides, and implementing measures such as increasing rodent predator populations such as raptors (Singleton *et al.*, 2010).

Raptor populations are controlled by bottom-up or top-down processes, and depends on the life-history traits of prey species which are critical in transferring contaminants across trophic levels (Baudrot *et al.*, 2018). In certain raptor species, such as the golden eagle (*Aquila chrysaetos*), where no environmental contaminants were considered, reproductive performance was shown to be determined by bottom-up processes with little evidence of top-down control of small mammal prey populations (Schmidt *et al.*, 2018). Whereas in species such as the barn owl (*Tyto alba*), soil contaminant toxicity such as of cadmium, determines the effect on trophic cascade regulation on food chain stability (Baudrot *et al.*, 2018). It was found that soil cadmium toxicity under threshold limits weakened food chain resilience, and at higher concentrations of soil cadmium contaminants, top-down control is triggered over small mammal prey populations (Baudrot *et al.*, 2018). As a result, a top-down control over small mammal prey can be expected in agricultural landscapes which are considerably contaminated with chemical phytosanitaries compared to natural habitats (Şekercioğlu, 2004).

Several empirical studies show that raptor abundance has the potential to regulate rodent densities (Muñoz-Pedreros *et al.*, 2010; Luna *et al.*, 2020; Montoya *et al.*, 2021) such that it is plausible to assume that raptors have the potential to control rodent populations (Donázar *et al.*, 2016). In line with the modern IPM schemes, current studies show that the habitat complexity of agricultural lands has been increased to provide optimal foraging grounds for raptors to control rodent populations, in addition to providing artificial nest sites to facilitate the predation of rodents by raptors (Muñoz-Pedreros *et al.*, 2010; Luna *et al.*, 2020). Therefore, there is a call for less aggressive environmental exploitation to be able to sustain biodiversity in agroecosystems and benefit from natural ecosystem services (Donázar *et al.*, 2016).

1.1.2 Raptors as structuring agents of biological communities

Raptors can also aid in structuring biological communities (Sergio *et al.*, 2007; Valkama *et al.*, 2005). Intraguild predation, which is the killing and consumption of species that share similar resources (Polis and Holt, 1992), is a widely occurring phenomenon amongst raptors (Solonen, 2011). Being apex predators, raptors can act as both potential competitors and predators with other species of raptors with similar foraging habits that can lead to a restructured raptor assemblage (Solonen, 2011). For example, Sergio *et al.* (2007) showed that spatial gaps in tawny owl (*Strix aluco*) distribution because of predator avoidance behaviour in response to eagle owls (*Bubo bubo*), indirectly favoured other owl species, thereby resulting in a diverse owl community. Similarly, Lourenço *et al.* (2011) showed that super predation (the act of killing and eating another predator) among the goshawk (*Accipiter gentilis*), golden eagle (*Aquila chrysaetos*), Bonelli's eagle (*Aquila fasciata*) and eagle owl was a response to a decrease in the main prey of these raptors, leading to a restructured raptor community. Therefore, raptors can facilitate changes in their species assemblages. Regardless of intraguild predation, raptors are also shown to structure communities of other species through predation pressure; For example, red grouse (*Lagopus scoticus*) populations in Scotland declined when raptors occurred at high density because of red grouse abundance, a top-down process resulting in the reduction of both the breeding density and productivity of red grouse (Thirgood *et al.*, 2000). Therefore, raptors can not only aid in structuring biological communities but can also act as an indicator of ecosystem health.

1.1.3 Scavenging and removal of animal carcasses

Raptors help in the removal of animal carcasses and facilitate nutrient cycling (Donázar *et al.*, 2016). Scavenging by raptors not only facilitates nutrient cycling, but the removal of animal carcasses prevents the attraction of unwanted predators such as red foxes (*Vulpes vulpes*) which might carry diseases such as rabies (Peisley *et al.*, 2017). For example, scavenging vultures (Accipitridae and Cathartidae) in Kenya are shown to triple the decomposition rate of carcasses, thereby reducing the time available for mammal scavengers to feed on carcasses and potentially reducing the risk of disease transmission (Ogada *et al.*, 2012). Furthermore, scavenging raptors have shown the potential to recognise novel food items (Beckmann and Shine, 2011). For example, in the Australian wet-dry tropics, raptors such as black kites (*Milvus migrans*) and whistling kites (*Haliastur sphenurus*) have readily consumed the tongue of invasive cane toads (*Bufo marinus*) when native frog populations were low in abundance (Beckmann and Shine, 2011). Thus, raptors provide several ecosystem services and are an important indicator of ecosystem health.

1.2 Global decline of raptor populations

Global decline in raptor populations is a result of anthropogenic activities that include, but are not limited to, destruction and alteration of habitats through agriculture and logging (Grande *et al.*, 2018), human-raptor conflicts (Canney *et al.*, 2022), and climate change (Wichmann *et al.*, 2003; Iknayan and Beissinger, 2018).

1.2.1 Agriculture and logging

Since the 1700s, agricultural land has expanded fivefold because of the Industrial Revolution and the advancement of technologies associated with the rapid growth of human societies (Ellis *et al.*, 2010). At present, most of the agricultural land operates either under monocultures or monoculture rotations thereby resulting in decreased landscape heterogeneity (Gámez-Virués *et al.*, 2015). Landscape homogenisation because of agricultural intensification can be detrimental to biodiversity. For example, agricultural intensification can destroy the habitat of raptor prey species, reduce breeding resources, and can also result in unintentional poisoning (Grande *et al.*, 2018). In a 12-year study in farmland landscapes in Western France, Butet, Rantier and Bergerot (2022) found that a generalist species such as the buzzard (*Buteo buteo*) showed a decline in abundance because of the lack of nest sites, whereas kestrels (*Falco tinnunculus*) suffered a decline in abundance because of small mammal prey depletion. However, on the positive side, the changes associated with agricultural intensification can result in novel breeding habitats and prey species, and perhaps even reduce competition between raptor species (Grande *et al.*, 2018). For example, the establishment of large open habitats for agriculture in the past may have provided new foraging and breeding habitats for harrier species in Europe and Central Asia (García *et al.*, 2011). Similarly, trees planted in farms can provide shade and shelter from natural elements such as wind thereby increasing the structural complexity of the landscape and consequently providing breeding opportunities, roosting and feeding spaces in otherwise unsuitable habitats (Zalba and Villamil, 2002). Human-induced changes in agriculture can also alter small mammal population dynamics thereby increasing the availability of prey to raptors (Caradador *et al.*, 2012). For example, Caradador *et al.* (2012) show that irrigated crops have a higher abundance of small mammal species than non-irrigated crops, potentially supporting western marsh-harrier (*Circus aeruginosus*) populations. Therefore, understanding the response of farmland raptors to agriculture can help in the implementation of appropriate actions to improve raptor conservation in the future.

The use of pesticides in agriculture has also contributed to a decline in raptor populations in the past. In particular, the use of dichloro-diphenyl-trichloroethane or commonly known as DDT had disastrous collateral effects on raptors, where DDT resulted in eggshell thinning, cracked eggs and an increase in egg destruction by parents (Porter and Wiemeyer, 1969; Hartley and Douthwaite, 1994; Falk *et al*. 2018). While many countries in the world banned the use of DDT in the 1970's, the long-lasting effects of DDT remain to this day. For example, Falk *et al.* (2018) shows eggshell thinning in present-day Greenlandic peregrines (*Falco peregrinus*) that can consequently impact breeding success. Similarly, the use of a veterinary anti-inflammatory drug such as diclofenac has resulted in mortalities of several scavenging species such as vultures in India, where high residues of diclofenac were found along with visceral gout in vulture corpses (Shultz *et al.*, 2004). However, with the consequent ban on the use of diclofenac in 2008, the decline in vulture populations has slowed (Prakash et al., 2012). Therefore, despite the direct effects of agriculture on farmland raptors, the use of pesticides and livestock drugs has contributed to raptor declines in the past, with some of its effects carried on to the current day.

Global agricultural expansion-driven habitat loss and fragmentation can negatively impact raptor populations (Panopio *et al.*, 2021). For example, the destruction of natural habitats has resulted in isolated populations, restricted gene flow, reduced ranges and even extirpation of raptors (Panopio *et al.*, 2021). Deforestation in the neotropical regions is particularly problematic, resulting in range reductions thereby threatening many raptor species (Miranda *et al.*, 2021). For example, the feeding rates and the nesting success of the harpy eagle (*Harpia harpyja*) showed a rapid decrease with an increase in forest loss (Miranda *et al.*, 2021). For viable reproduction of harpy eagle pairs, the authors further suggested that at least 50% of forest cover is required in the Amazon, which is undergoing deforestation at an increased rate. Despite deforestation having a direct impact on raptor sustenance, deforestation can further result in conflicts between raptors and humans (Restrepo-Cardona *et al.*, 2019). For example, the black-and-chestnut eagle (*Spizaetus isidori*) preyed more on domestic fowl in deforested habitats creating raptor-human conflict, while mammals were the most dominant prey for the black-and-chestnut eagle in forest-covered regions of the Andean landscapes in Colombia (Restrepo-Cardona *et al.*, 2019). Deforestation has negative effects not only on raptors, but can further extend and exacerbate human-wildlife conflicts, and must therefore be prevented. The prevention of deforestation has strong established links with indigenous people, where there is a focus on reconciliation of land and resource use rights of the indigenous people in protected areas (Gavin *et al.*, 2018). For example, land management by indigenous communities in the neotropical areas has resulted in the efficient protection of forests from deforestation compared to forest loss in nationally protected areas (Schleicher *et al.*, 2017). Furthermore, raptor research projects have benefitted from using indigenous knowledge and engagement (Vargas González and Vargas, 2011). For example, harpy eagle nest monitoring efforts in many South American countries have been effective because of the participation of indigenous communities, where the indigenous people contributed by locating harpy eagle nests surrounding their community (Vargas González and Vargas, 2011). Therefore, to mitigate the effects of deforestation on raptor populations, a socioecological approach is warranted as deforestation in indigenous lands is currently an ongoing issue in relation to biodiversity conservation.

1.2.2 A short summary of human-raptor conflicts

An increase in intentional and unintentional anthropogenic disturbances has negatively impacted raptors worldwide (McClure *et al.*, 2018). Intentional anthropogenic practices such as poisoning, shooting and trapping, unintentional anthropogenic disturbances such as urbanisation, and the construction of wind turbines and powerlines remain to be persistent threats to raptor survival (McClure *et al.*, 2018; Kettel et al., 2018). For example, Cianchetti-Benedetti *et al.* (2016) showed that 52% of all Falconiformes admissions to wildlife rehabilitation centres in Rome, Italy, was because of shooting, while a study by Panter *et al.* (2022) showed that the number of admissions of raptors to rehabilitation centres in the United Kingdom because of vehicular collisions was the highest followed by building collisions. Vehicular collisions were especially high among common buzzards (*Buteo buteo*), mainly because buzzards scavenge road-killed animals (Schwartz *et al.*, 2018).

Apart from hunting and collisions, the electrocution of raptors is another cause for concern in raptor conservation (Slater, Dwyer and Murgatroyd, 2020). Raptors can get electrocuted when there is contact between two live uninsulated wires of differing electric potential, or when there is contact between a live uninsulated wire and a path to the ground (Slater, Dwyer and Murgatroyd, 2020). This causes larger raptors such as Spanish imperial eagles (*Aquila adalberti*) to be disproportionately killed by electrocution (48-60% mortalities; González *et al.*, 2007). To mitigate the effects of electrocution on raptors, several measures have been suggested, amongst which, the use of insulation is widely practised (Slater, Dwyer and Murgatroyd, 2020). Other measures include providing platforms for raptors to perch, conducting risk assessments and removing raptor nests during powerline inspections (Slater, Dwyer and Murgatroyd, 2020).

Finally, wind turbine farms are also shown to contribute to raptor mortality (Smallwood and Thelander, 2008; de Lucas *et al.*, 2012; Martínez-Abraín *et al.*, 2012; Watson, 2018). Unlike collisions with stationary buildings, moving blades of wind turbines pose a threat to flying raptors as there are limited sensory cues provided for raptors to make behavioural adjustments (Hunt and Watson, 2016). In addition, some migratory raptors are known to avoid proximity to wind turbines (Johnston, Bradley and Otter, 2014). Several solutions have been suggested to avoid future raptor-wind turbine collisions, ranging from using less lethal turbine blades, to installing sensors that stop the turbines when raptors are within close proximity (Watson, 2018). Overall, unintentional persecution of raptors is going to be a continued cause for the decline in raptors because of the destruction of natural habitats to meet the needs of a growing human population.

1.3 Raptor conservation challenges

Human activities such as urbanisation and intensive agriculture have accelerated biodiversity decline worldwide (McKinney, 2002; Dudley and Alexander, 2017). However, information on many of the threats to biodiversity, and species' response to ecosystem changes because of anthropogenic disturbance are still very limited (Xu *et al.*, 2018). In general, most raptors occur in low population densities and are difficult to detect, making them unfeasible to study (Newton, 1979). As a result, most of the research occurs where there is funding available for the most visible or "charismatic" raptor species (cf. Griffiths and Dos Santos, 2012; Martín-López, González and Montes, 2011). However, the disparity in research attention on threatened raptor species can be attributed to high levels of social inequality and poverty, with most of the research occurring in developed parts of the world such as in Europe and North America compared to where the regions of the world of high priority, such as in the neotropics and Southeast Asia (Velasco *et al.*, 2015). For example, Buechley *et al.* (2019) showed that one-fifth of global raptor species had zero research publications, while only 1.8% of raptors received one-third of the research attention. In particular, Buechley *et al.* (2019) showed that raptor species with smaller range sizes occurring in less developed countries were the least studied, as these raptors tend to be habitat specialists, thus are harder to detect and study. Furthermore, raptor species with smaller range sizes, such as those inhabiting the islands of Southeast Asia, were also the ones prone to a higher risk of extinction as they occurred in small population sizes, so are vulnerable to stochastic changes in the environment (Sodhi *et al.*, 2010). Similarly, raptor species that are dependent on forested regions (Nearly 80% of all raptor species) are also at a high risk of extinction compared to raptors utilising other habitats (McClure *et al.*, 2018). Overall, information on the imminent threats to understudied raptor species remains scarce.

Among all types of raptors, owls (Strigiformes) are the least studied raptor species and require urgent conservation investment after vultures, which are the most extinction-prone raptor species (Buechley *et al.*, 2019). Globally, nearly 50 species of owls are threatened by agriculture and logging, compared to an approximate 40 species of hawks and eagles, 3 species of falcons, and 7 species of old-world vultures (Buechley *et al.,* 2019), highlighting the importance of studying owls.

Raptor conservation benefits from global, multi-species monitoring programs (Lindenmayer, Piggott and Wintle, 2013), but such monitoring programs involve aggregation, dissemination, and summarisation of scientific material to aid in the future conservation of raptors (McClure *et al.*, 2021). Several initiatives have been established (Davies and Virani, 2013; Perrig *et al.*, 2019; McClure *et al.*, 2021) which have now taken a collaborative approach to increase the efficacy of global raptor monitoring (McClure *et al.*, 2021). For example, the Global Raptor Information Network (GRIN) was first started in the 1990s to report the breeding biology, conservation status and migratory patterns of all diurnal raptor species (McClure *et al.*, 2021). Users of GRIN can contribute observations of raptors along with information such as the height of flight, raptor species, types of behaviour, sex, age, colour morphs, time of observation, mortalities, etc. (McClure *et al.*, 2021). An application of the data collected by GRIN is reported in Sutton *et al.* (2021), where a 11% reduced range for harpy eagles is reported. Therefore, GRIN has the analytical capabilities to contribute to various aspects of raptor research ranging from risk assessments to raptor monitoring.

1.4 Raptors in the United Kingdom – status, threats, and research prospects

In the United Kingdom, raptors currently face several human-induced challenges compared to natural challenges, such as vehicular/building collisions, habitat destruction, fencing, entanglements and electrocution (Panter *et al.*, 2022). However, in the past, raptor numbers suffered greatly because of agricultural intensification and agriculture-induced pesticide poisoning (Newton, 2004). Post-war Britain saw a dramatic increase in agriculture to attain self-sufficiency in food production (Robinson and Sutherland, 2002). As a result, farming was commercialised which resulted in a 65% decrease in small farms, and a 50% removal of hedgerows, which is vital for the sustenance of a majority of farmland biodiversity (Robinson and Sutherland, 2002). Lack of breeding habitats and prey resulted in a decline in raptor populations; for example, common kestrels (*F. tinnunculus*) and the barn owl (*Tyto alba*) suffered greatly because of the lack of nesting sites such as old trees and the reduction in small mammal prey (Newton, 2004). A few farmers erected fences to prevent overgrazing by sheep to protect rough grasslands and promote small mammal populations, and in addition, licensed bird ringing volunteers installed artificial nest boxes to facilitate the recovery of kestrel and barn owl populations in the late 1970s (Newton, 2004). Furthermore, the Environmental Stewardship Scheme was introduced in 2005, which resulted in the protection of substantially large areas of rough grassland and grass margins that provided breeding habitats for raptors such as the barn owl and facilitated the growth of small mammal populations (Askew, Searle and Moore, 2007a).

With intensified commercial farming post the second world war came the extensive use of fertilisers and pesticides such as dichlorodiphenyltrichloroethane (DDT), which further led to the mortalities of raptors because of poisoning and reproductive failures (Ratcliffe, 1967; Shore and Taggart, 2019). For example, the impact of DDT on reproduction in raptors was tested in captive birds and the detrimental results were used to reduce and finally ban the use of DDT in agriculture by 1986 (Newton, 2004). Although alternative rodenticides such as the second-generation anticoagulant rodenticides (SGAR) are currently used to control rodent populations, the impact of SGARs on raptor survival remains inconclusive. For example, a study by Knopper *et al.* (2007) found no evidence that sub-lethal exposure of SGARs to raptors affected the bone density of raptors. However, a recent study found a negative correlation between the use of SGARs and the annual abundance of kestrel populations, the mechanism for which remains unknown (Roos *et al.*, 2021). Despite these threats in the recent past, raptor populations in the United Kingdom have continued to grow and persist because of the implementation of several conservation strategies and reintroduction programs (Stanbury *et al.*, 2021). For example, Project Barn Owl initiative by the British Trust for Ornithology along with the Breeding Bird Survey programs showed that the breeding population of barn owls has increased by 228% between 1995 and 2020 in the United Kingdom (Harris *et al.*, 2021). Similarly, another case study on peregrine falcons showed a 22% increase in breeding populations between 2002 and 2014 in the United Kingdom (Wilson *et al.*, 2018). Overall, raptor monitoring programs in the United Kingdom is shown to satisfactorily represent the status of breeding raptor populations through concerted conservation efforts compared to other European countries (Derlink *et al.*, 2018).

1.5 Barn owl as a conservation flagship in agricultural landscapes

The barn owl (*Tyto alba*) belongs to the family *Tytonidae*, part of the genus *Tyto* and is one of the most widespread and widely distributed owl species, present on every continent except Antarctica (Winkler, Billerman and Lovetter, 2020). As an apex predator with a cosmopolitan distribution, barn owls make an ideal model species with over 4000 scientific papers published globally in the field of Ecology and Conservation to date (Roulin, 2020).

1.5.1 Habitat and nesting preferences

The barn owl is an adaptable species that can be found in a wide range of habitats, from farmlands, grasslands and interspersed woodlands (Roulin, 2020). In the United Kingdom, barn owls are particularly drawn to lowland farmlands and open countryside due to the abundance of potential nesting sites and reliable food supple of small mammals like voles and mice (Fuller, Hinsley and Swetnam, 2004). Barn owls also show a preference for nesting in man-made structures such as old barns (hence the name 'barn' owls) and abandoned buildings (Martínez and Zuberogoitia, 2004). These structures provide secure and sheltered nesting sites, protecting the owls and their offspring from adverse weather conditions and potential predators (Shawyer, 1987). At present, conservation efforts have been directed towards providing artificial nest boxes to supplement suitable nesting sites and bolster barn owl populations in the UK (Newton, 2004). Overall, the habitat and nesting preferences of the barn owl shows a strong affinity to man-made structures and artificial nest boxes in areas with limited natural nesting sites.

1.5.2 Feeding behaviour and diet

Barn owls are nocturnal raptors with highly specialised feeding behaviour and a diverse diet that primarily consists of small mammals. As nocturnal hunters, barn owls rely on their exceptional low-light vision and acute hearing to locate and capture prey in darkness (Mikkola, 2014). Their facial disk acts as an acoustic funnel, allowing them to capture and focus sound waves, which aids in locating potential prey (Payne, 1971). They primarily hunt from elevated perches or during low-level flight over agri-environment scheme farmlands, actively scanning the ground for movement and sounds that signal the presence of potential prey (Séchaud *et al.*, 2021).

In agricultural landscapes, barn owls exhibit remarkable flexibility in their foraging behaviour, adapting to changes in prey availability and seasonal variation in agriculture (Kross, Bourbour and Martinico, 2016). During periods of high small mammal abundance, barn owls take advantage of the plentiful prey and increase their hunting activity (Séchaud *et al.*, 2021). In addition, they are also shown to modify their home range to focus on areas with higher concentrations of small mammals (Séchaud *et al.*, 2022). Barn owls also adjust their hunting behaviour based on seasonal changes in agricultural landscapes such that during the harvest season, barn owls hunt in fields with standing crops, and after the harvest, they target stubble fields where small mammals seek cover (Séchaud *et al.*, 2021).

The diet of the barn owl is predominantly composed to small rodents, such as voles, mice and shrews, which are actively hunted in grasslands, farmlands, and wetlands (Glue, 1974). In addition to rodents, barn owls occasionally consume other small mammals, such as bats, reptiles and small birds (Glue, 1974; Meek *et al*., 2009; Roulin and Dubey, 2012). The diverse diet of barn owls makes them highly effective predators and are used to control rodent populations in agricultural landscapes (Meyrom *et al*., 2009; Kan *et al*., 2014; Kross, Bourbour and Martinico, 2016; Johnson *et al*., 2018).

1.5.3 Reproduction and breeding

Barn owl reproduction and breeding is characterised by monogamous pair bonding, where males secure one female at a time (Roulin, 2020). During the breeding season, male barn owls court potential mates through vocalisations and aerial displays, and once a pair is formed, they work together to establish a nesting site, which often involve man-made structures such as old barns and farm buildings (Roulin, 2020). Barn owls typically breed once or twice a year, and their breeding is influenced by prey availability, availability of nesting sites and weather conditions (Taylor, 1994; Chausson *et al*., 2014).

The female barn owl lays a clutch of eggs ranging from three to seven eggs, and the incubation period typically lasts around 30 to 34 days, during which the male barn owl provides food for the female barn owl which remains dedicated to keeping the eggs warm (Howell, 1964; Smith, Wilson and Frost, 1974). After hatching, the chicks are altricial, meaning they require constant care from their parents, and food is provided until the chicks are ready to fledge and become independent (Smith, Wilson and Frost, 1974).

The number of eggs laid by the female barn owl is influenced primarily small mammal reproductive cycles, a dominant food type of barn owls (Roulin, 2020). The breeding patterns of small mammals, such as voles and mice are shown to be influenced by food availability, temperature, and day length (Batzli, 1992). Adequate food resources are essential for female small mammals to reach optimal body condition, as well as for the survival and growth of their offspring, such that abundant food periods result in larger litter sizes and more frequent breeding events (Korpimäki *et al*., 2004). Temperature also plays a critical role in small mammal reproduction, such that warmer temperatures often advance the onset of breeding (Lewellen and Vessey, 1998). Lastly, the day length or photoperiod acts as a crucial cue for the initiation of reproductive activities in small mammals. The lengthening or shortening of daylight hours triggers hormonal changes that influence the timing of breeding, with longer daylight hours in spring being favourable for small mammal reproductive activity (Walton, Weil and Nelson, 2011). Being opportunistic predators, barn owls adjust their breeding timing to coincide with peak small mammal abundance, ensuring a readily available food source for their chicks during the demanding nesting period (Horváth, Bank and Horváth, 2020). Overall, barn owl breeding is intrinsically linked to reproductive cycles of small mammals, with the timing and breeding success of barn owls being closely tied to the availability of their primary prey.

1.5.4 Barn owl conservation status in the United Kingdom

The global conservation status of the barn owl varies across different regions and countries. The International Union for Conservation of Nature (IUCN) classifies the barn owl as a species of “Least Concern” on the global scale, indicating that barn owls are not currently facing a high risk of extinction worldwide (International

Union for Conservation of Nature, 2019). However, it is important to note that the conservation status of barn owls can vary regionally, and populations in certain areas face more significant threats. In the United Kingdom, barn owl is considered to be a species of "conservation concern" due to habitat loss, pesticide use, and reduced prey availability (Newton, 2004).

Habitat loss and degradation are significant threats to barn owl populations. Agricultural intensification, and land-use changes have led to the destruction of traditional nesting sites such as tree cavities and reduced the availability of suitable hunting grounds (Hindmarch *et al.*, 2012). Additionally, the removal of hedgerows and old buildings diminishes the nesting opportunities and roosting sites for barn owls (Newton, 2004). Finally, the use of rodenticides and pesticides in agriculture also poses a significant threat to barn owls through secondary poisoning because of ingestion of contaminated prey, leading to population declines (Newton and Wyllie, 2002).

Among all raptors in the United Kingdom, barn owls have been extensively studied, mainly because of their widespread distribution in the United Kingdom and globally, and because of their past decline in population numbers (barn owl studies on: land use, Bond *et al.*, 2005 and Meek *et al.*, 2009; diet, Love *et al.*, 2000 and Askew, Searle and Moore, 2007b; Agri-environment scheme, Askew, Searle and Moore, 2007a; human intervention, Ramsden, 1998 and Meek *et al.*, 2003). Agro-environment schemes and environmental stewardship schemes have played a vital role in barn owl conservation in the United Kingdom (Askew, Searle and Moore, 2007a). Under these schemes, farmers are encouraged to create and maintain barn owl-friendly habitats such as grasslands with unharvested field margins and rough grassland areas, which provide essential foraging grounds and nesting sites for barn owls (Vickery *et al.*, 2004). In addition, both schemes also encourage creating wildflower margins, small-mammal friendly features such as log piles and establishing hedgerows to provide essential cover, foraging areas, and nesting sites for small mammals, the dominant prey of barn owls (Broughton *et al.*, 2014). Finally, other conservation initiatives such as the installation of artificial nest boxes in landscapes with intensive agriculture has ensured the stability of barn owl populations (Newton, 2004). Overall, these conservation initiatives demonstrate the value of collaborative efforts between agricultural practices and wildlife conservation to support farmland biodiversity, including barn owls in the United Kingdom.

1.5 Aims of study

In this first nationwide initiative, this thesis examines the impact of agriculture on the reproductive potential of barn owls (*Tyto alba*) in agricultural landscapes of maize, wheat, barley, potato, fruit and forage crops, sugar beet, oilseed rape and root crops of Great Britain. In addition, this thesis also examines the impact of four commonly used pesticides in the cultivation of the most dominant crop type in Great Britain, cereal crops, on barn owl reproductive potential. Previously, studies on barn owl reproduction in response to land use have been spatially restricted (Bond *et al.*, 2005; Meek *et al.*, 2009). Whereas this study makes use of barn owl breeding data archived by the British Trust for Ornithology between 2012 – 2016 across the Midlands, South East and South West of Great Britain, which vary in the intensity of agriculture (further justification and rationale are provided in Chapter 2). The results of this thesis will provide an understanding of the effects of agriculture on barn owl reproduction across a vast spatial extent in Great Britain, thereby facilitating informed agri-environmental scheme implementation for the conservation of farmland biodiversity.

In particular, this PhD thesis aims to:

1) **Examine barn owl reproduction in response to agricultural landscape composition across the Midlands, South East and South West of Great Britain.** In Chapter 2, I aim to examine patterns in barn owl brood size and nestling body mass in response to agricultural landscape composition defined by metrics such as total land use (total crop area), habitat fragmentation (number of crop patches), habitat complexity (perimeter:area ratio) and crop diversity.
2) **Determine the impact of landscape composition of cereal crops on maternal barn owl body condition and reproduction.** In Chapter 3, I aim to determine the impact of cereal crop landscape composition, the most dominant crop type in the United Kingdom, on maternal barn owl body condition (using a scaled body mass index) and consequently examine the effects of maternal barn owl body condition on barn owl brood size and nestling body mass. Brood size of barn owls is used as a proxy for barn owl productivity while nestling body mass is used as a proxy for body condition of barn owl nestlings.

3) **Examine the indirect effects of pesticide use on barn owl reproduction.** In Chapter 4, I examine the effects of four commonly used herbicides (glyphosate and flufenacet) and fungicides (chlorothalonil and diflufenican) in the cultivation of cereal crops, the most dominant crop type in Great Britain, on barn owl brood size and nestling body mass.
4) **Determine the diet of breeding barn owls in Great Britain.** In Chapter 5, I determine the diet of breeding barn owls in the Midlands and the South East, as barn owl brood sizes significantly differ between the Midlands and the South East (see Chapters 2 for details). Furthermore, the effect of the landscape composition of cereal crops, the most dominant crop type in Great Britain, on the barn owl diet is examined. Barn owl reproductive potential is predominantly influenced by food availability during breeding (Durant, Gendner and Handrick, 2004). Therefore, in this study, I present dietary data identified to the Order level in relation to the frequency of occurrence of barn owl prey items, and examine the dietary overlap of barn owls in the two regions that differ in the agricultural intensity of cereal crops, Midlands and the South East. Finally, I present the relationship between the landscape composition of cereal crops and the diet of the barn owl.

1.6 Thesis structure

This thesis uses barn owls as model species to investigate the impact of the current agricultural land use on raptor reproduction (see Fig. 1.1). In Chapter 2, I provide a detailed introduction on previous trends in barn owl reproduction and how all these studies are on a local scale. Next, I proceed to compare the intensity of agriculture between the three regions of Great Britain, the Midlands, South East and the South West from where the barn owl data originate, and to examine whether there is difference in the intensity of agriculture. Then, I use generalised linear mixed models to predict barn owl brood size and nestling body mass of barn owls in agricultural lands with different crop types. Finally, I simulate barn owl brood sizes from generalised linear mixed models to verify the predictive power of agricultural landscape composition in determining barn owl brood size. The results from Chapter 2 are a precursor to Chapters 3 and 4, where I explore different aspects of barn owl reproduction, and further examine effects of agriculture on barn owl reproduction.

In Chapter 3, I examine the effects of the agricultural landscape composition of cereal crops, the most dominant crop type in Great Britain, on maternal barn owl body condition and consequently on barn owl brood sizes. Here, I present evidence from the published literature that barn owl reproductive output is dependent on maternal barn owl body condition, and therefore test whether the agricultural landscape composition of the most dominant cereal crop in Great Britain impacts maternal barn owl body condition compromising on reproductive output (barn owl brood size). Here I construct generalised linear mixed models using proxies such as land use of cereal crops, habitat fragmentation and habitat complexity interacting with maternal barn owl body condition to predict barn owl brood sizes and nestling body mass of barn owls. Similar to Chapter 2, I simulate barn owl brood sizes to establish the strength of the interaction of landscape composition metric of cereal crops and maternal barn owl body condition in predicting barn owl brood sizes.

In Chapter 4, I present evidence on how pesticide use associated with agricultural intensification has previously affected farmland raptor species resulting in breeding failures, including the barn owl. Furthermore, I discuss the limitations of the current approval procedures of candidate pesticides for commercial use by presenting examples of the indirect effects of herbicides and fungicides on raptor health and reproduction. Next, I use four commonly used herbicides (glyphosate and flufenacet) and fungicides (chlorothalonil and diflufenican) to predict barn owl brood size and nestling body mass of barn owls using generalised linear models. Finally, I simulate barn owl brood sizes (similar to Chapter 2 and Chapter 3) to establish the strength of pesticide use in predicting barn owl brood sizes using the candidate pesticide which has a significant impact on barn owl brood size.

In Chapter 5, I examine the diet of barn owls in the Midlands and the South East of Great Britain which differ in the intensity of agriculture. Barn owl reproductive potential is predominantly influenced by food availability during breeding (Durant, Gendner and Handrick, 2004). Here I present the dietary composition of the barn owl in the Midlands and the South East, and also examine the extent of overlap in barn owl diet between the Midlands and the South East.

Finally, in Chapter 6, I discuss how barn owl reproduction is not influenced by a single environmental factor, but rather by an interplay between barn owl biology and environmental factors that influences barn owl reproductive potential. Furthermore, I provide suggestions on the ideal landscape structure in farmlands that would be beneficial for breeding barn owl populations and how the barn owl can act as a conservation flagship for the protection of all farmland biodiversity.

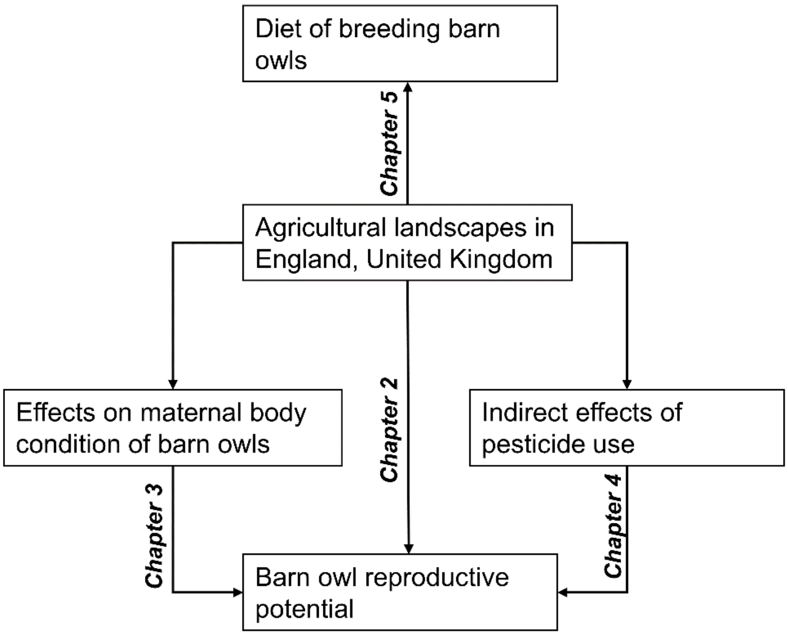

Figure 1. 1. Flowchart highlighting the structure of the thesis. Although the diet of breeding barn owls influences barn owl reproductive potential, breeding data associated with diet records were not available for further analysis.

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Chapter 2

Ghosts of barn owls past: Impact of agricultural landscape composition on barn owl breeding performance in Great Britain

2.1 Abstract

Land use in previous studies has been shown to be a poor predictor of barn owl reproduction, suggesting that barn owls find suitable foraging habitats that do not compromise their capability to reproduce. However, spatially widespread studies on the impact of agricultural landscape composition on barn owl breeding are lacking. In this study, the relationship between agricultural landscape composition and 561 barn owl breeding attempts (361 nest boxes) from three distinct geographical regions across Great Britain were analysed using generalised linear mixed models (GLMM). Irrespective of region, an increase in the total area of fruit/forage crops had a positive impact on barn owl productivity, resulting in large brood sizes. On a regional level, large areas of cereal crop fields, comprising a small number of patches, resulted in small barn owl brood sizes with higher average body mass of nestlings in the Midlands compared to the South East, but not the South West of Great Britain. Furthermore, GLMM simulations showed that landscape composition metrics by themselves do not accurately predict barn owl breeding, but these findings suggest that a reduction in barn owl brood size occurs in cereal crop dominated agricultural landscapes without compromising the body condition of barn owl nestlings. Consequently, current intensive cereal crop cultivation in large homogeneous fields is restricting barn owl productivity.

Keywords

Intensive agriculture; farmland raptor; brood size; cereal crop; body condition; productivity

2.2 Introduction

Global changes in land use patterns are often a result of land encroachment for development purposes, such as urban expansion and agricultural intensification, to suit the needs of a growing human population (Foley *et al.*, 2005). Modern intensive agriculture can impact landscape structure through reduced habitat heterogeneity, which is detrimental to biodiversity (Vickery and Arlettaz, 2012). For example, loss of mixed farming practices can result in a decreased range of habitat types and associated niches for farmland raptors such that it is detrimental to raptor populations (Atuo and O'Connell, 2017). Intensive agriculture can also impact the reproductive performance of raptors (Väli, 2017). For example, large areas of oilseed rape fields and mowed cultivated grasslands in Estonia had a negative impact on the reproductive performance of lesser spotted eagles *Clanga pomarina* (Väli, 2017). Raptors in general provide critical ecosystem services such as agricultural production (natural pest control) and waste-disposal (through scavenging) in anthropogenic environments (O'Bryan *et al.*, 2018). Overall, unfavourable agricultural practices and habitat destruction are the most common causes of declining raptor populations (McClure *et al.*, 2018).

Post second world war, the volume of agricultural output (crop produce and livestock) in the United Kingdom rose by 255% between 1945 and 1980 (Brassley, 2000), and farmland bird populations suffered dramatic declines (Newton, 2004). At present, nearly 75% of UK land is devoted to agriculture, with cereal crops dominating at 52% of UK farmland (Department for Environment, Food and Rural Affairs, 2017; 2019a). Conseqently, farmland breeding bird populations have declined by 45% since the 1970s, and the current decline in farmland birds could also be attributed to rapid changes in agricultural land use regimes between 1986 and 2011, which resulted in a decrease in grassland footprint and an increase in cropland footprint (Department for Environment, Food and Rural Affairs, 2019b; de Ruiter *et al.*, 2017).

A farmland raptor species that has suffered greatly in population numbers in the past is the barn owl (*Tyto alba*), having declined by 70% between 1932 and 1985 from 12,000 to 4,440 breeding pairs in the United Kingdom, mainly because of habitat loss and unregulated use of organochlorine pesticides in farming (Shawyer, 1987; Newton, 2004). As a result of this decline in barn owl population numbers, conservation measures ranging from installation of nest boxes to the introduction of Agro-Environment Schemes, have aided in barn owl population recovery in the UK (Meek *et al.*, 2003; Askew, Searle and Moore, 2007). For example, nest box provision and habitat protection have been predominantly increased alongside introduction of captive-bred barn owls to the wild to recover barn owl populations in the UK (Ramsden and Ramsden, 1989; Toms, Crick and Shawyer, 2001). Under the Agro-Environment Schemes, farmers are encouraged to create and maintain barn owl-friendly habitats such as grasslands with unharvested field margins and rough grassland areas, which provide essential foraging grounds and nesting sites for barn owls (Vickery *et al.*, 2004; Askew, Searle and Moore, 2007). Altogether, these conservation measures have increased the breeding population of barn owls by 228% between 1995 and 2020 in the UK (Harris *et al.*, 2021).

Barn owls exhibit a high degree of flexibility in their life history strategies allowing them to persist in a wide range of habitats, including man-made and altered habitats (Roulin, 2020). For example, barn owls have been reported to forage beyond their home ranges (~1km radius around the nest site) when the immediate habitat around the nest site is not suitable for foraging (Taylor, 1994; Shawyer, 1998). There have also been instances where male barn owls in Swtizerland have travelled as far as ~20km away from their nest sites while foraging (Séchaud *et al.*, 2022). Barn owls in Europe are reported to have a varied diet and are opportunistic feeders, which aids their survival (Bernard *et al.*, 2010; Roulin and Dubey, 2012; Roulin and Christe, 2013). However, barn owls are prone to declines in numbers if the area of rough grassland around nest sites is below ~9ha, climatic conditions deteriorate, and prey populations decline (Shawyer, 1998). In addition, Bond *et al.* (2005) showed that unsuccessful barn owl breeding attempts were linked to an abundant presence of improved grassland, suburban land and wetlands. Despite these findings, much of what is known about barn owl breeding performance in relation to land use in the UK has been derived from studies that are spatially restricted to the South East of England, representing 36% of the total area of England (Bond *et al.*, 2005; Meek *et al.*, 2009).

The role of land use in barn owl breeding performance was last studied in the UK by Meek *et al.* (2009), who reported that breeding performance in relation to land use and habitat was similar to that expected by chance. Similar findings were reported by Frey *et al.* (2011), where barn owl reproductive success in Switzerland was not related to any agricultural landscape variables, including crop area. Indeed, both Meek *et al.* (2009) and Frey *et al.* (2011) suggest that barn owls can find suitable foraging habitats around nest boxes to aid their survival. However, the geospatial data on land use used by Frey *et al.* (2011) does not correspond entirely to the time-period during which the nests were monitored, which might have resulted in spurious results in relation to barn owl reproduction, whereas the study by Meek *et al.* (2009) was spatially restricted to the south Midlands (~20% of the total area of England). What remains to be established is whether there are general trends in barn owl reproduction at a multiscale level in relation to current agricultural land composition that can aid in implementing conservation measures both at a regional and national level.

In this chapter, a nationwide study is carried out to determine the impact of agricultural landscape composition metrics of five major crop types on barn owl brood size (proxy for reproductive performance) and average body mass of barn owl nestlings (proxy for body condition of nestlings), from three distinct geographical regions, the Midlands, South East and South West of Great Britain. First, the impact of agricultural landscape composition - total area, number of patches and perimeter:area of different crop types on barn owl brood size were compared using generalised linear mixed models and model selection procedures proposed by Burnham and Anderson (2002). Second, the crop types that best explained differences in barn owl brood size were selected, and the agricultural landscape composition metrics of the selected crop types were compared to evidence the differences in agricultural landscape composition between the three regions. Finally, the impact of agricultural landscape composition metrics of the selected crop types were used to determine the impact on the average body mass of barn owl nestlings. I hypothesise that the differences in the intensity of agriculture on between the three geographical regions impact barn owl brood sizes differentially, such that agricultural landscape homogeneity (e.g. larger total area and a smaller number of crop patches of a given crop type) has a negative impact on barn owl reproduction, resulting in small barn owl brood sizes. Agricultural landscape homogeneity can therefore result in a trade-off between the number of offspring that fledge (smaller barn owl brood sizes) and their corresponding body condition (conserved body mass of nestlings). The findings from this study will aid in developing effective conservation strategies for farmland raptors such as the barn owl.

2.3 Materials and methods

2.3.1 Barn owl breeding data

Archived data from the British Trust for Ornithology (BTO) comprising a total of 561 breeding attempts from 361 unique nest boxes were used. The data were naturally clustered across three regions in Great Britain; the Midlands (n = 133 breeding attempts; 106 nest boxes), South East (n = 302; 192), and South West (n = 126; 63) of Great Britain from 2016 – 2018 (Fig. 2.1). The Brood size (a proxy for productivity) and the corresponding average body mass of nestlings (a proxy for body condition of nestlings) corrected for brood size, and corresponding to age code 1 - juveniles of the BTO bird ringing code were obtained for each breeding attempt. A total of 157 nest boxes were used two to three times between 2016 – 2018; 27 nest boxes in the Midlands, 85 nest boxes in the South East, 45 nest boxes in

South West. Whether the nest boxes were used multiple times (twice or thrice) by the same individual barn owl was not considered. Furthermore, none of the nest boxes were used more than once for breeding in the same year between 2016 – 2018. Finally, the average body mass of barn owl nestlings per nest box was available for a subset of the total data (n = 324/361) and was used as a direct measure of the body condition of barn owl nestlings.

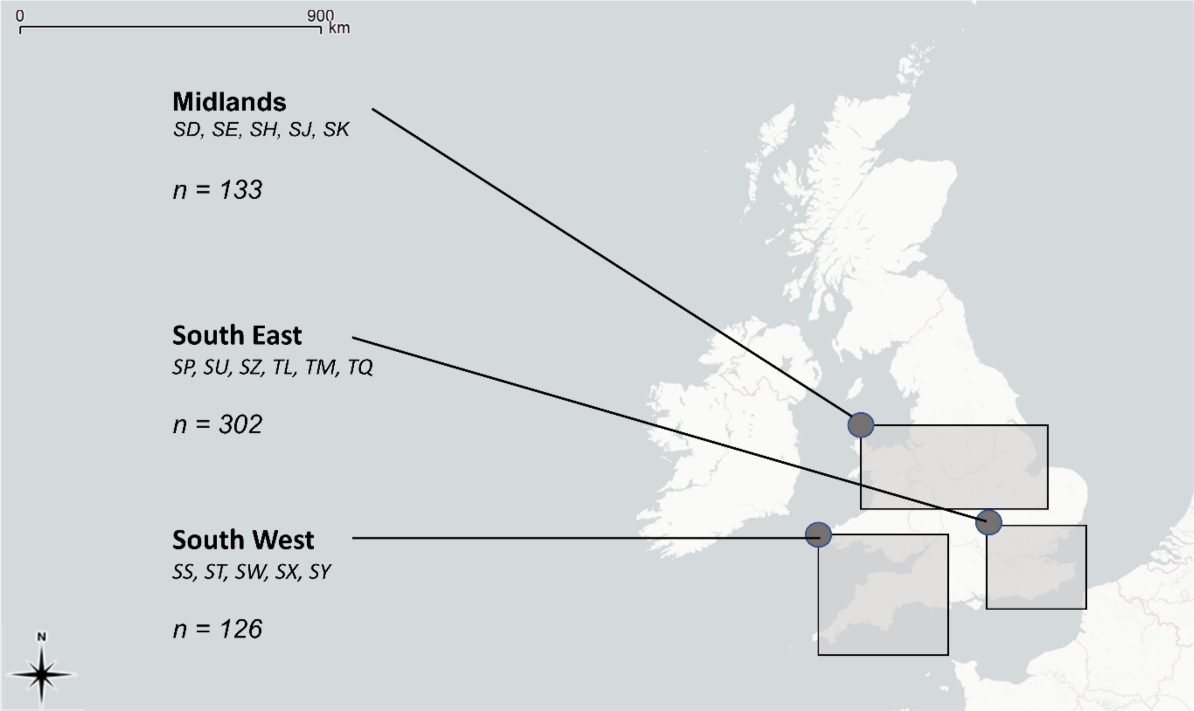

Figure 2. 3. Map of the United Kingdom showing the three regions between which brood size of barn owls were compared. The grey boxes show the extent of the distribution of nest boxes within each region. British National Grids corresponding to the nest box locations and sample numbers are also provided.

2.3.2 Geospatial data on agricultural land use and landscape structure

Geospatial data on crop cover for Great Britain published by the Centre for Ecology and Hydrology (CEH Land Cover® Plus: Crops, 2016; 2017; 2018) were used to predict barn owl brood size and the average body mass of barn owl nestlings in relation to agricultural landscape composition in the UK. The crop cover data is classified into 10 different crop cover categories: winter wheat, spring wheat, winter barley, spring barley, maize, sugar beet, potatoes, field beans, oilseed rape and ‘other’, where ‘other’ comprises root crops, early potatoes and vegetables; plus, an 11th ‘improved grasslands’ land use category, which comprises intensively managed and highly modified agricultural grasslands. The crop cover categories winter wheat, spring wheat, winter barley, spring barley and maize were grouped based on vegetation structure and seasonal phenology to form the category ‘cereal crops’, while ‘other’ crops which consists of fruit and forage crops were renamed ‘fruit/forage crops’, and ‘field beans’ were renamed ‘pulse crops’. Sugar beet and potato categories were omitted from analyses as they represented <10% of the land around nest boxes considered in this study. Overall, the five crop groups retained for analysis were cereal crops, improved grassland, oilseed rape, fruit/forage crops and pulse crops.

A buffer of 1km radius (3.14km^2) was constructed around each nest box to represent the home range of barn owls (Bond *et al.*, 2005; Meek *et al.*, 2009; Frey *et al.*, 2011; Hindmarch *et al.*, 2012). Within each buffer, three different landscape composition metrics were calculated for each representative crop cover type (Table 2.1): total area (land use metric), number of patches (habitat fragmentation metric), and perimeter:area ratio (habitat complexity metric). In addition, Simpson’s diversity index, a proxy for crop diversity, was calculated around each nest box. Simpson’s diversity index was preferred over other diversity indices such as Shannon’s diversity index because the sampling was considered to be complete, as all major crop types were included. Furthermore, Shannon’s diversity index is used only if the richness of the number of land use types within the focal area is greater

Table 2. 3. Landscape composition metrics used to analyse agricultural landscape composition of each crop type around each nest box in the Midlands, South East and South West of Great Britain. All landscape composition metric definitions are taken from McGarigal and Marks (1995).

Landscape composition metric	Proxy for	Definition	In literature
Total area of crop cover	Land use	Total area equals the sum of the areas (m^2) of all individual patches of the corresponding crop type, divided by 10,000 (to convert to hectares). Larger area represents more of the land use type.	Wilson, Johnson and Bissonette (2009); Pereira, Saura and Jordán (2017); Kim, Eui Choi and Chon (2018); Herse, With and Boyle (2020); Morante-Filho, Benchimol and Faria (2020)
Number of patches per crop type	Habitat fragmentation	The number of patches per crop type. More patches represent higher habitat fragmentation.	Carrara *et al.* (2015); Mortelliti *et al.* (2010); Thornton, Branch and Sunquist (2011); Hiron *et al.* (2015); De Camargo, Boucher – Lalonde and Currie (2018)
Perimeter:area ratio	Habitat complexity	The ratio of the patch perimeter (m) to area (m^2) of the corresponding crop type. Higher perimeter:area ratio represents more complex habitats.	Sanz-Pérez *et al.* (2019); Zingg *et al.* (2019); Pretelli, Isacch and Cardoni (2018); Dixon, Baker and Ellis (2020); Sutti, Strong and Perlut (2017)
Simpson's diversity index	Crop cover diversity	Simpson's diversity equals 1 minus the sum, across all crop types, of the proportional abundance of each crop type squared, calculated for each nest box. Higher diversity index represents higher species diversity.	Bond *et al.* (2005); Oja, Alamets and Pärnamets (2005); Katayama *et al.* (2014); Ke *et al.* (2018)

than 100 (Herzog *et al.*, 2001). All GIS analyses were carried out using the landscape ecology statistics plugin (LecoS; Jung, 2016) for QGIS v2.18.0 (QGIS Development Team, 2009).

2.3.3 Statistical analyses

The impact of agricultural landscape composition on barn owl brood size was determined by undertaking generalised linear mixed models for each crop type (n = 5) with a Conway-Maxwell Poisson distribution (CMP) and loglambda link function (glmmTMB R package; Brooks *et al.*, 2017). A CMP distribution was used to deal with under dispersion of the response variable brood size of barn owls (Shmueli *et al.*, 2005; Sellers and Shmueli, 2010). To examine the impact of agricultural landscape composition on barn owl brood size (response variable), total area, number of patches and perimeter:area ratio of each crop type were modelled as predictors with region included as an interaction effect with each metric. The year of nest use between 2016 – 2018 was included as a random effect in all five crop type models. A null model was constructed for barn owl brood size and included the intercept and the year of nest use as the random effect. Model dredging procedure was not undertaken as dredging can result in spurious results of no biological significance (Smith, 2002; Burnham and Anderson, 2002). Instead, model selection procedures of $\Delta AIC_c < 2$, described by Burnham and Anderson (2002), were used to retain crop cover models that best explained differences in brood size (MuMIn R package; Bartoń, 2022). Kruskal-Wallis tests alongside Mann-Whitney U pairwise comparisons were undertaken to compare the differences in landscape composition metrics of crop cover models which had a $\Delta AIC_c < 2$.

The impact of agricultural landscape composition on the average body mass of barn owl nestlings (non-normal distribution; Shapiro-Wilk's test: $W = 0.94$, $P < 0.001$) was determined by undertaking generalised linear mixed models with a Gamma distribution with log link function (lme4 R package; Bates *et al.*, 2015) for crop type models with a $\Delta AIC_c < 2$ in predicting barn owl brood sizes. When barn owl broods require extra parental effort, a reduction in brood size occurs with an increase in the body mass of nestlings to ensure their survival (Roulin, Ducrest and Dijkstra, 1999). As brood size and body mass of nestlings are correlated, landscape composition metrics (total area, number of patches and perimeter:area ratio) interacting with region of crop cover models which had a $\Delta AIC_c < 2$ in predicting barn owl brood sizes were used to model the average body mass of barn owl nestlings. The year of nest use between 2016 – 2018 was included as a random effect in all models.

Finally, two generalised linear mixed models with Gamma distribution and log link function were constructed to examine the impact of crop diversity between regions (with region included as an interaction with Simpson diversity index) on barn owl brood size and the average body mass of barn owl nestlings with the year of nest use between 2016 – 2018 included as a random effect.

Landscape composition metrics are correlated to a certain extent, and the introduction of interaction effects in models tend to increase the variance inflation factor (VIF) of predictors (Robinson and Schumacker, 2009). Therefore, VIF of individual effects were verified to be <10 for all models (see example - Ohashi *et al.*, 2020). Finally, the residual plots were visually assessed for similar variance across treatments and the impact of influential outliers for all GLMMs was carried out using the DHARMa R package (Hartig, 2022). Influential outliers with Cook's distance greater than one were removed from the analysis.

To verify the predictive power of the selected GLMMs, model coefficients with the corresponding confidence intervals were used to simulate (n = 10,000) the percentage of occurrence of the most frequently observed barn owl brood size in the dataset and compared to the actual occurrence of the most frequently observed brood size in the dataset (Zuur and Ieno, 2016). Simulations were only carried out if at least one of the terms in the selected GLMM was significant. All data analyses were carried out in R v3.6.2 (R Core Team, 2019).

2.4 Results

Among all five crop types and the null model, fruit/forage crops and cereal crops were the best predictors of barn owl brood sizes ($\Delta AIC_c < 2$; Table 2.2). The landscape composition of fruit/forage crops; total area ($\chi^2 = 3.17$, df = 2, P = 0.197), number of patches ($\chi^2 = 0.02$, df = 2, P = 0.986), and perimeter:area ratio ($\chi^2 = 4.17$, df = 2, P = 0.118), was not significantly different between the Midlands, South East and the South West of Great Britain. However, the landscape composition of cereal crops; total area ($\chi^2 = 22.48$, df = 2, P < 0.001), number of patches ($\chi^2 = 13.36$, df = 2, P < 0.001), and perimeter:area ratio ($\chi^2 = 35.01$, df = 2, P < 0.001), differed significantly between the Midlands, South East and the South West of Great Britain (Fig. 2.2).

Mann-Whitney pairwise comparisons showed that the total area of cereal crops was significantly greater in the Midlands (median ± interquartile range: 121.39

Table 2. 2. Generalised linear models with Conway-Maxwell Poisson distribution and loglambda link function predicting barn owl brood size. Fruit/forage crops and cereal crops were the only models with $\Delta AIC_c < 2$ and are in bold. AIC_c – Sample corrected Akaike information criteria, ΔAIC_c – Difference between the model with the lowest AIC_c and the candidate model, ω_i – Akaike weight (Burnham and Anderson, 2002).

Model	**Deviance**	**Log likelihood**	**AIC_c**	**Δ AIC_c**	ω_i
Fruit/Forage crops	**1600.3**	**-800.1**	**1629.06**	**0**	**0.60**
Cereal crops	**1601.4**	**-800.7**	**1630.1**	**1.07**	**0.35**
Improved grassland	1607.1	-803.5	1635.8	6.7	0.02
Null model	1630.6	-815.3	1636.6	7.6	0.01
Oilseed crops	1608.2	-804.1	1636.9	7.8	0.01
Pulse crops	1611.6	-805.8	1640.3	11.2	0.002

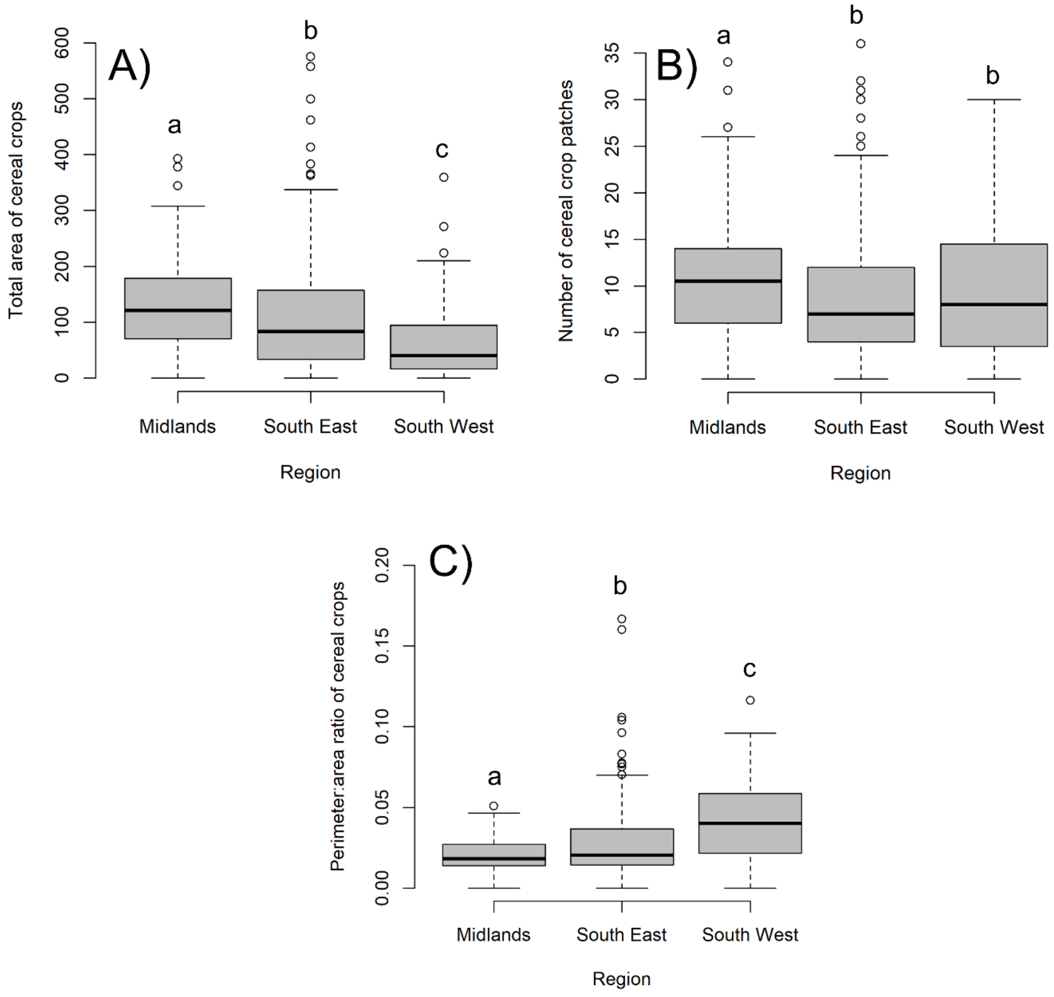

Figure 2. 4. Landscape composition of cereal crops between the Midlands, South East and the South West of Great Britain. A) Differences in total area of cereal crops B) Differences in number of cereal crop patches, and C) Differences in the perimeter:area ratio of cereal crops between the three regions of Great Britain. The bold line of the boxplot represents the median, the shaded region represents the interquartile range, the error bars show the minimum and maximum values, and the circles represent outliers. The lowercase letters above the boxplot represents significant differences between the three regions of Great Britain.

± 109.32, compared to the South East (U = 8573; P = 0.024) and the South West (U = 1852; P < 0.001), which also differed significantly from each other, with the South East (83.5 ± 123.81) having greater total area of cereal crops compared to the South West (40.61 ± 81.12; U = 4412.5; P < 0.001; Fig. 2.2). The number of patches of cereal crops was significantly greater in the Midlands (10.5 ± 8) compared to the South East (U = 7496.5; P < 0.001) but not the South West (U = 2850; P = 0.111), and the South East (7 ± 8) and the South West (8 ± 12) did not differ significantly from each other (U = 5606; P = 0.383; Fig. 2.2). Finally, the perimeter:area ratio was significantly higher in the South West (0.04 ± 0.03) compared to the South East (U = 3757.5; P < 0.001) and the Midlands (U = 1500; P < 0.001), which also differed significantly from each other, with the South East (0.02 ± 0.02) having higher perimeter:area ratio than the Midlands (0.01 ± 0.01; U = 8639; P = 0.031; Fig. 2.2).

2.4.1 Landscape composition predictors of barn owl brood size

Fruit/forage crops and cereal crops were the best predictors of barn owl brood sizes ($\Delta AIC_c < 2$; Table 2.2). Regardless of the region, the number of patches of fruit/forage crops had a significant positive impact on barn owl brood size. Larger brood sizes were significantly predicted by a greater number of fruit/forage crop patches ($\beta = 0.048$, $CI_{95} = 0.006, 0.09$; z = 2.24, P = 0.024; Fig. 2.3). The total area of fruit/forage crops, and perimeter:area ratio of fruit/forage crops, did not significantly predict barn owl brood size by themselves and between regions (Table 2.3). The model variance of fruit/forage crops explained by the random effect - year was very low; the interclass-correlation coefficient was 0.007, conditional R^2 was 0.028 and the marginal R^2 was 0.021.

On a regional level, large brood sizes were significantly predicted by a small total area of cereal crops, comprising a greater number of patches in the Midlands (Intercept - $\beta = 1.307$, $CI_{95} = 1.077, 1.537$; $z = 11.13$, $P < 0.001$; Fig. 2.4a), which differed significantly from a larger area of cereal crops ($\beta = 0.002$, $CI_{95} = 0.0001, 0.003$; $z = 2.17$, $P = 0.029$) comprising a smaller number of patches ($\beta = -0.038$, $CI_{95} = -0.064, -0.013$; $z = 2.96$, $P = 0.003$; Fig. 2.4b) in the South East, but not the South West of Great Britain (Table 2.3; Fig. 2.4). The total area of cereal crops (pairwise contrasts based on means; t-ratio = 1.72, $P = 0.198$) and number of cereal crop patches (pairwise

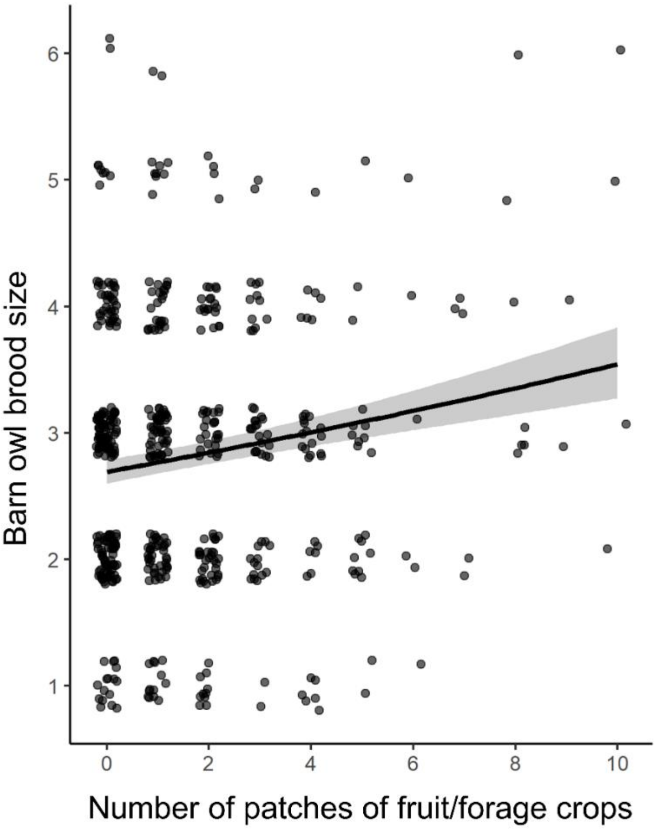

Figure 2. 3. Conway – Maxwell Poisson distribution GLMM of fruit/forage crops, showing the relationship between the number of patches of fruit/forage crops and barn owl brood size, irrespective of region. An increase in the number of patches of fruit/forage crops contributed to larger barn owl brood sizes. Shaded areas represent 95% confidence intervals.

Table 2. 4. Generalised linear mixed models with Conway-Maxwell Poisson distribution and loglambda link function predicting barn owl brood size. Fruit/forage crops and cereal crops were the only models with $\Delta AIC_c < 2$ and are in bold. The intercept corresponds to the Midlands, and individual effects of number of patches, perimeter:area ratio and total area are presented in the row corresponding to the intercept. 95% Confidence intervals are provided within parentheses and significant interactions are in bold. ICC – Intraclass correlation coefficient, R^2 (Cond.) – R^2 Conditional, R^2 (Marg.) – R^2 Marginal.

Model	Region	Intercept	Total area (ha)	Number of patches	Perimeter:area ratio	Random effect - year		
						ICC	R^2 (Cond.)	R^2 (Marg.)
Fruit/forage crops	Intercept	1.002 (0.886, 1.117)	-0.0005 (-0.005, 3.822)	**0.04 (0.006, 0.09)**	-0.87 (-5.572, 3.822)	0.007	0.028	0.021
	South East	-0.04 (-0.161, 0.072)	-0.001 (-0.007, 0.004)	-0.04 (-0.097, 0.011)	3.51 (-1.57, 8.588)			
	South West	0.08 (-0.05, 0.211)	0.001 (-0.015, 0.018)	-0.04 (-0.161, 0.067)	0.49 (-5.532, 6.527)			
Cereal crops	Intercept	1.307 (1.077, 1.537)	-0.002 (-0.003, -0.0005)	0.01 (-0.0002, 0.039)	-11.59 (-24.045, 0.848)	0.004	0.024	0.021
	South East	-0.23 (-0.479, 0.011)	**0.002 (0.0001, 0.003)**	**-0.03 (-0.064, -0.013)**	12.91 (0.164, 25.672)			
	South West	-0.19 (-0.457, 0.063)	0.001 (-0.002, 0.004)	-0.009 (-0.043, 0.025)	9.3 (-4.031, 22.641)			
Null model	Intercept	1.03 (0.988, 1.085)	-	-	-	0.003	0.003	0.001
Pulse crops	Intercept	1.07 (0.986, 1.162)	-0.002 (-0.008, 0.003)	0.03 (-0.053, 0.123)	0.401 (-3.637, 4.438)	0.003	0.018	0.014
	South East	-0.05 (-0.146, 0.042)	0.003 (-0.004, 0.106)	**-0.09 (-0.202, 0.013)**	0.49 (-3.865, 4.861)			
	South West	-0.00007 (-0.102, 0.102)	-0.01 (-0.022, 0.058)	-0.12 (-0.647, 0.391)	2.48 (-15.231, 20.197)			
Improved grassland	Intercept	1.05 (0.757, 1.355)	-0.001 (-0.002, 0.0005)	0.01 (-0.01, 0.039)	-0.001 (-0.002, 0.0005)	0.004	0.021	0.017
	South East	-0.284 (-0.674, 0.105)	**0.002 (0.0005, 0.004)**	-0.01 (-0.041, 0.016)	0.64 (-8.77, 10.06)			
	South West	0.04 (-0.881, 0.971)	0.0005 (-0.002, 0.003)	-0.009 (-0.046, 0.026)	0.8 (-34.331, 35.938)			
Oilseed rape	Intercept	1.13 (1.014, 1.258)	0.00007 (-0.002, 0.002)	0.01 (-0.034, 0.071)	-6.46 (-12.705, -0.231)	0.002	0.02	0.017
	South East	-0.12 (-0.254, -0.0004)	-0.001 (-0.006, 0.002)	-0.03 (-0.124, 0.06)	**7.48 (0.264, 14.698)**			
	South West	-0.03 (-0.169, 0.101)	0.003 (-0.008, 0.016)	-0.03 (-0.187, 0.118)	2.8 (-5.009, 10.62)			

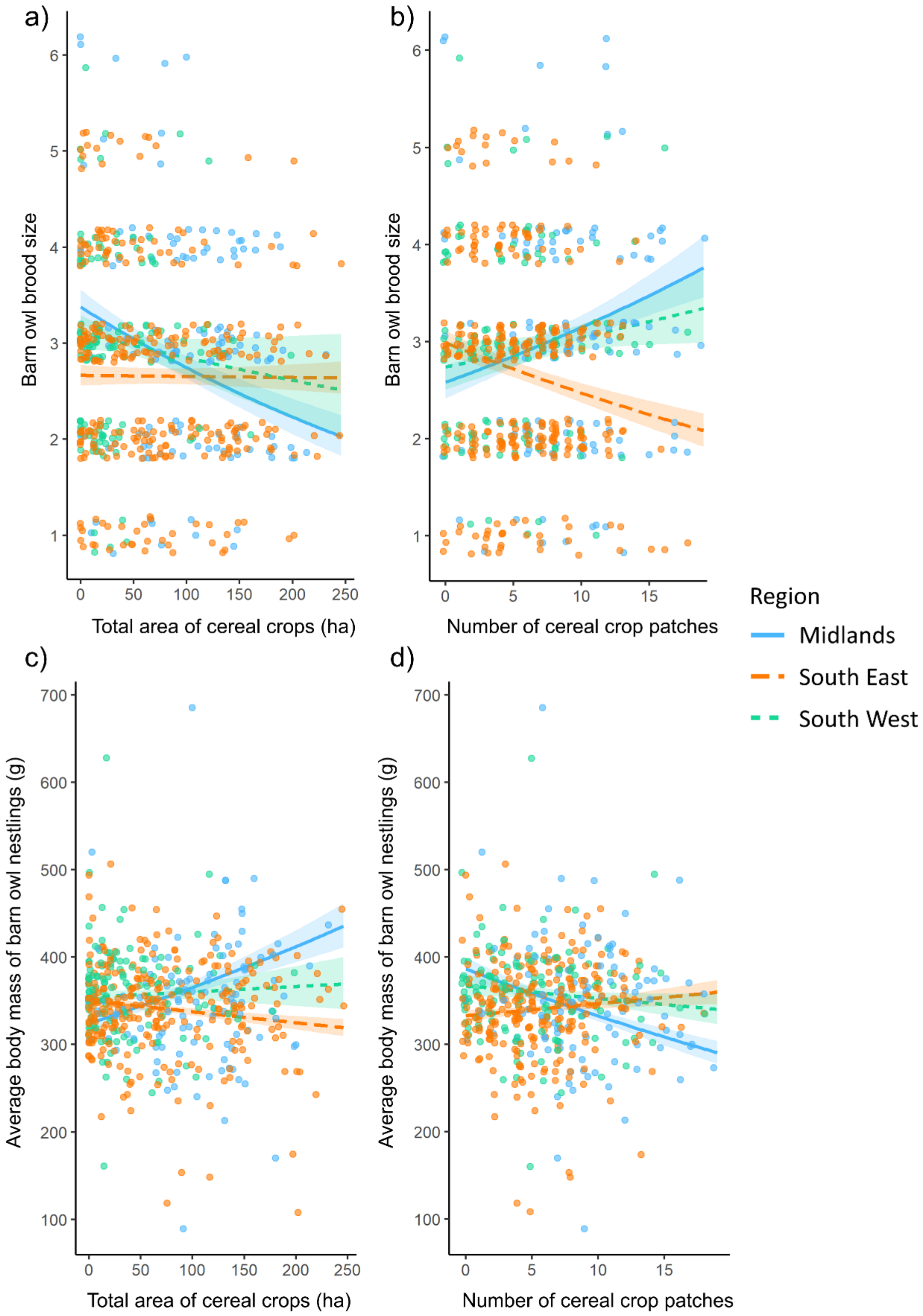

Figure 2. 4. Relationship between (a) the total area of cereal crops (ha) and barn owl brood size (b)the number of cereal crop patches and barn owl brood size in the cereal crop Conway-Maxwell Poisson distribution GLMM. Relationship between (c) the total area of cereal crops (ha) and average body mass of barn owl nestlings (d) the number of cereal crop patches and average body mass of barn owl nestlings in the Gamma distribution GLMM.

contrasts based on means; t-ratio = 1.72, P = 0.198) did not significantly predict barn owl brood size between the South East and the South West. The perimeter:area ratio of cereal crops had no significant effect on the brood size of barn owls (Table 2.3). Finally, the model variance of cereal crops explained by the random effect - year was very low; the interclass-correlation coefficient was 0.004, conditional R^2 was 0.024 and the marginal R^2 was 0.021.

Crop diversity (Simpson diversity index) did not significantly predict barn owl brood size between regions (Table 2.4a).

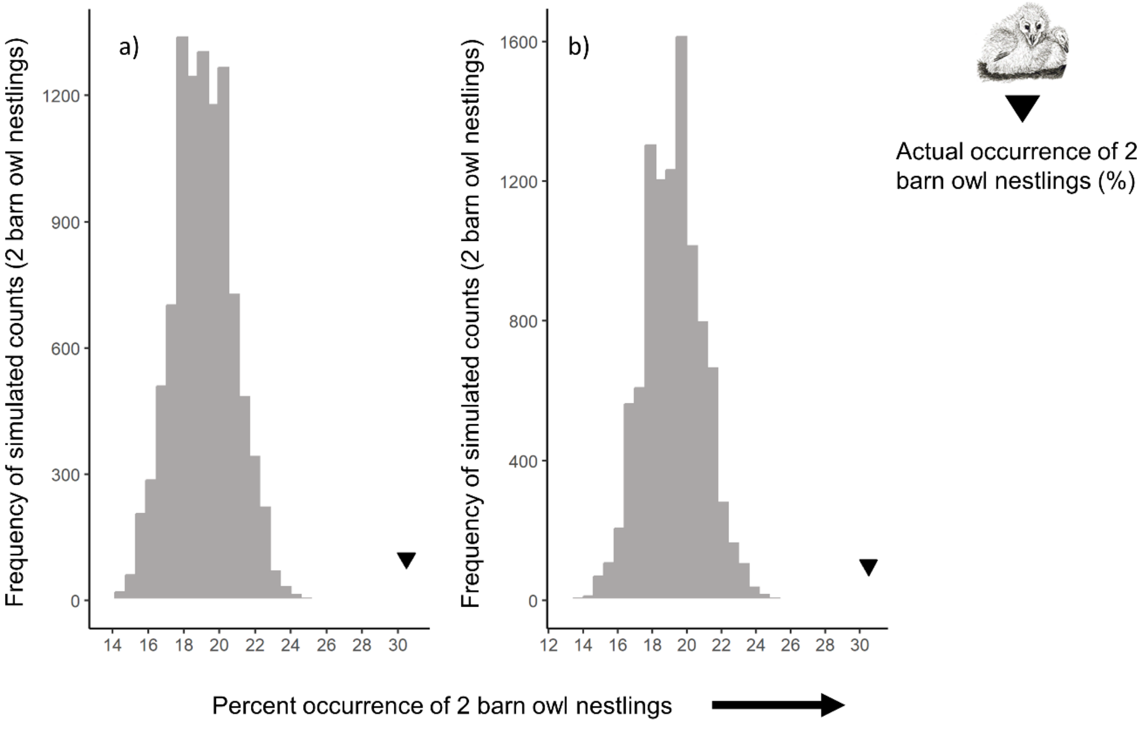

Figure 2. 5. Histogram showing the occurrence of simulated brood size of two barn owl nestlings using the model coefficients of a) fruit/forage crop GLMM, b) cereal crop GLMM. The actual percentage of occurrence of two barn owl nestlings observed in the dataset (31%) lies outside the range of the simulated barn owl brood size of two barn owl nestlings, suggesting that barn owl brood size is not reflected by agricultural land use alone.

The most frequently observed brood size in the dataset was two barn owl nestlings per nest box. The percent occurrence of simulated brood size of two barn owls ($n = 10,000$) for the fruit/forage crops and cereal crops GLMM ranged from 14-25% and 13-25%, respectively. However, the actual percent occurrence in the dataset was 31% ($n = 561$), which lies outside the simulated ranges of 14-25% and 13-25%, suggesting that the fruit/forage crops and cereal crops GLMM underestimated the percent occurrence of a brood size of two barn owl nestlings (Fig. 2.5). Therefore, despite being retained as a good fit compared to other crop type models in Table 2.2, the fruit/forage crops and cereal crops GLMMs do not accurately reflect barn owl brood size accurately in terms of predictive power, suggesting that barn owl brood size is not influenced by agricultural land use alone, and can be influenced by other factors relating to prey deliveries by male barn owls and female body condition.

2.4.2 Landscape composition predictors of barn owl nestling body mass

None of the measures of fruit/forage crops (total area, number of patches and perimeter:area) significantly predicted the average body mass of barn owl nestlings (Table 2.4a). An increase in the average body mass of barn owl nestlings was significantly predicted by a larger total area of cereal crops which comprised a smaller number of patches around nest boxes in the Midlands (Intercept - $\beta = 5.75$, $CI_{95\%} = 4.32, 6.86$; $t = 69.41$, $P < 0.001$; Fig. 2.5), which differed significantly from a smaller total area of cereal crops ($\beta = -0.001$, $CI_{95\%} = -0.002, -0.0005$; $t = 3.04$, $P = 0.002$) comprising a greater number patches ($\beta = 0.01$, $CI_{95\%} = 0.005, 0.03$; $t = 2.79$, $P = 0.005$; Fig. 2.5d) in the South East, but not the South West (Table 2.4a). The total area of cereal crops (post hoc Tukey; t-ratio = 2.08, $P = 0.092$) and the number of cereal crop patches (post hoc Tukey; t-ratio = 2.08, $P = 0.092$) did not significantly predict the

Table 2. 4. (a) Generalised linear mixed models with Gamma distribution and log link function predicting the average body mass of barn owl nestlings. The intercept corresponds to the Midlands, and individual effects of number of patches, perimeter:area ratio and total area are presented in the row corresponding to the intercept. (b) Generalised linear mixed model with Conway-Maxwell Poisson distribution and loglambda link function predicting barn owl brood size, and a generalised linear mixed model with Gamma distribution and log link function predicting the average body mass of barn owl nestlings using crop diversity (Simpson's diversity index) as a predictor. 95% Confidence intervals are provided within parentheses and significant interactions are in bold. ICC – Intraclass correlation coefficient, R^2 (Cond.) – R^2 Conditional, R^2 (Marg.) – R^2 Marginal.

a)

Model	Region	Intercept	Total area (ha)	Number of patches	Perimeter:area ratio	Random effect - year		
						ICC	R^2 (Cond.)	R^2 (Marg.)
Fruit/forage crops	Intercept	5.84 (5.784, 5.9)	-0.0004 (-0.003, 0.002)	0.004 (-0.021, 0.029)	0.508 (-2.068, 3.085)	0.005	0.026	0.022
	South East	-0.02 (-0.088, 0.034)	0.0007 (-0.002, 0.004)	0.001 (-0.031, 0.033)	-0.307 (-3.154, 2.539)			
	South West	0.03 (-0.032, 0.102)	0.0006 (-0.003, 0.004)	-0.008 (-0.046, 0.029)	0.05 (-3.082, 3.183)			
Cereal crops	Intercept	5.75 (5.591, 5.916)	0.001 (0.0002, 0.002)	-0.01 (-0.025, -0.004)	6.52 (-1.546, 14.593)	0.005	0.044	0.04
	South East	0.09 (-0.073, 0.263)	**-0.001 (-0.002, -0.0005)**	**0.01 (0.005, 0.032)**	-7.31 (-15.554, 0.904)			
	South West	0.13 (-0.041, 0.302)	-0.001 (-0.002, 0.0004)	0.01 (-0.229, 0.248)	-5.98 (-1.814, 11.545)			

b)

Model	Region	Intercept	Simpson's diversity index	Random effect - year		
				ICC	R^2 (Cond.)	R^2 (Marg.)
Barn owl brood size	Intercept	1.16 (0.975, 1.349)	-0.11 (-0.381, 0.153)	0.003	0.022	0.019
	South East	0.0008 (-0.203, 0.205)	-0.22 (-0.536, 0.089)			
	South West	-0.09 (-0.3, 0.118)	0.15 (-0.212, 0.531)			
Average body mass of barn owl nestlings (g)	Intercept	5.88 (5.759, 6.002)	-0.04 (-0.211, 0.124)	0.005	0.023	0.018
	South East	-0.04 (-0.175, 0.081)	0.03 (-0.151, 0.225)			
	South West	0.01 (-0.11, 0.145)	-0.007 (-0.214, 0.199)			

average body mass of barn owl nestlings between the South East and the South West. The perimeter:area ratio of cereals crops had no effect on the average body mass of barn owl nestlings (Table 2.4a). The model variance of cereal crops explained by the random effect - year was very low; the interclass-correlation coefficient was 0.005, conditional R^2 was 0.044 and the marginal R^2 was 0.04.

Crop diversity (Simpson diversity index) did not significantly predict the average body mass of barn owl nestlings between regions (Table 2.4b).

2.5 Discussion

In this first large-scale study on barn owl reproduction, hierarchical generalised linear models were constructed to determine the impact of agricultural landscape composition on barn owl reproductive performance (brood size of barn owls) and nestling body condition (the average body mass of barn owl nestlings) in Great Britain. It was found that fruit/forage crops and cereal crops are the best predictors of barn owl brood size and the average body mass of barn owl nestlings in the UK.

Irrespective of region, it was found that a greater number of fruit/forage crop patches has a positive impact on barn owl brood size, resulting in large brood sizes. Fruit/forage crop fields are intensively managed through mechanical means (e.g. mowing of vegetation cover) and chemical means (e.g. use of herbicides; Sullivan, 2006). Intensive management practices of fruit/forage crops can result in a decline of small mammal populations, a reliable source of food for barn owls (Butet *et al*., 2006; Gelling *et al*., 2007), because of the loss suitable habitat for breeding (Shave, Lundrigan and Lindell, 2018). Despite intensive management practices in fruit/forage crop fields, the adjoining lands (or hedgerows, known as source area habitats) can contribute to small mammal population recovery and maintenance through immigration (Sullivan, 2006; Sullivan and Sullivan, 2009). Small mammal species such as *Microtus spp.* readily feed on the bark, vascular tissues, and the root of fruit/forage crops (Sullivan, 2006). Therefore, the relationship between small mammal populations in fruit/forage crop fields and adjoining source area habitats is such that fruit/forage crop provides food for small mammal populations whereas the adjoining land provides the ideal habitat for breeding and protection from predators. As a result, a greater number of fruit/forage crop patches can contribute to larger brood sizes because of the abundance of small mammal prey found in fruit/forage crop patches interspersed with source area habitats for small mammal populations that provides suitable habitat for breeding.

Next, it was found that cereal crops are the second best predictors of barn owl brood size after fruit/forage crops. In the United Kingdom, 75% of the land is devoted to agriculture, and farming is concentrated in the arable heartland of the English Midlands (Department for Environment, Food and Rural Affairs, 2019a, Ilbery *et al.*, 2016). Of the 75% of total cultivated land, 52% of cereal crops dominate the agricultural sector in Great Britain (Department for Environment, Food and Rural Affairs, 2017). Therefore, it is not surprising that the total area and number of patches of cereal crops was found to be the highest in the Midlands, compared to the South East and the South West. The habitat complexity (perimeter:area ratio) of cereal crops was the highest in the least intensive cereal crop cultivated region of the South West where livestock farming is predominant, compared to the Midlands and the South East (Department for Environment, Food and Rural Affairs, 2017). In the Midlands, large brood sizes were predicted by a small total area of cereal crops, comprising a greater number of patches compared to the South East, where the trend was the complete opposite, mainly because of the low intensity in cereal crop cultivation in the South East compared to the Midlands (small total area of cereal crops).

Intensive agriculture can result in a loss of natural habitats, which can be vital for the sustenance of small mammal populations (Butet *et al*., 2006). For example, Herldová *et al*. (2007) showed that small mammal abundance, a reliable food source for barn owls (Butet *et al*., 2006; Gelling *et al*., 2007), was lowest in cereal crops compared to permanent habitats such as windbreaks, small woods, and fallow land. Therefore, it is likely that high intensity of cereal crop cultivation in the Midlands (large total area of cereal crops) can result in smaller brood sizes compared to low intensity cereal crop cultivation regions of the South East and the South West (small total area of cereal crops). Next, a positive response of the total number of cereal crop patches on barn owl brood size in the Midlands compared to the South East and the South West can be associated with a greater number of linear features such as hedgerows and grass margins, which are vital in maintaining small mammal populations. For example, hedgerows are the sole habitats of small mammals such as the wood mouse *Apodemus sylvatics* and the bank vole *Clethrionomys glareolus* in intensively managed agricultural lands (Boone and Tinklin, 1988). Furthermore, Agro-Environment Schemes and Environmental Stewardship Schemes have played a vital role in barn owl conservation in the United Kingdom (Askew, Searle and Moore, 2007). Under these schemes, farmers are encouraged to create and maintain barn owl-friendly habitats such as grasslands with unharvested field margins and rough grassland areas, which provide essential foraging grounds and nesting sites for barn owls (Vickery *et al.,* 2004). In addition, both schemes also encourage creating wildflower margins, small-mammal friendly features such as log piles and establishing hedgerows to provide essential cover, foraging areas, and nesting sites for small mammals, the dominant prey of barn owls (Broughton *et al.,* 2014). In the South East and the South West, where livestock farming is more predominant than in the Midlands, loss of natural grasslands because of grazing practices can result in a consequent decline in small mammal populations, restricting barn owl productivity (Newton, 2004).

The body condition of nestlings increased with a larger total area of cereal crops comprising a small number of patches in the Midlands, whereas the opposite trend was found in the South East, but not the South West. Furthermore, the South East and the South West did not differ in predicting the average body mass of barn owl nestlings in cereal crop fields. Barn owl productivity depends on their feeding situation such that small brood sizes are a result of lack of food resources (Durant, Gendner and Handrich, 2010; Roulin, 2020). For example, Roulin, Ducrest and Dijkstra (1999) have shown that when barn owl broods require extra parental effort, a reduction in brood size occurs with an increase in the body mass of nestlings to ensure their survival. The current agricultural landscape composition of cereal crops in Great Britain can likely hinder barn owl foraging strategies such that a trade-off between food acquisition by males and a reduction in brood size by brooding females can occur (Durant, Gendner and Handrich, 2010). Therefore, larger total area of cereal crops comprising a small number of patches in the Midlands can limit barn owl brood sizes because of the lack of food resources such that all parental effort is concentrated on feeding a smaller brood to ensure nestling survival. Whether the current agricultural landscape in Great Britain negatively impacts the body condition of female barn owls because of the lack of prey resources resulting in reduced barn owl brood sizes, remains to be studied.

To attest the biological significance of fruit/forage crops and cereal crops GLMMs, predictive simulations were carried out using the model coefficients of the fruit/forage and cereal crop GLMMs, respectively. Both fruit/forage and cereal crop GLMM simulations showed that the simulated percent occurrence range of the most commonly occurring barn owl size (two barn owls), lay outside the percent actual occurrence of two barn owls nestlingsin the dataset. Here, it is shown that agricultural landscape structures alone are poor predictors of barn owl brood size.

Barn owl reproduction can be influenced by multiple factors which can range from climate (Chausson *et al*., 2014) to prey accessibility (Arlettaz *et al*., 2010) and prey availability (Bond *et al*., 2005). For example, Arlettaz *et al*. (2010) found that Swiss barn owls chose foraging habitats based on prey accessibility rather than prey abundance, and it is likely that the habitats around nest boxes in the Midlands and the South West are preferable than in the South East because of increased heterogeneity of habitat (greater number of patches) that makes prey accessibility easier for foraging barn owls, thereby producing larger barn owl brood sizes. What remains to be studied is whether the current agricultural landscape composition in the UK has a negative impact on barn owl foraging performance, such that it limits larger brood sizes because of the lack of food availability. Finally, it is recommended that future studies should not examine the relationship between agricultural landscape composition and species reproductive ecology alone, but in tandem with potential selection pressures that can limit or enhance reproductive productivity.

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Chapter 3

Landscape composition of cereal crops affects maternal barn owl body condition and reproduction

3.1 Abstract

Barn owl reproductive success has been typically linked to conditions during the pre-laying period, such as female body mass and male provisioning while brooding. Despite limited evidence that landscape composition of cereal crops is a determinant of barn owl reproduction, barn owls prefer to forage among cereal crop fields, compared to other crop types, irrespective of prey abundance. The potential mechanism of how the landscape composition of cereal crops impacts body condition, and in turn, the reproductive performance of barn owls, has been understudied. In this study, generalised linear mixed models were used to examine the impact of landscape composition of cereal crops on the body condition of female barn owls (n =126) and their subsequent reproductive performance (brood size and body condition of nestlings) in Great Britain. An increase in the number of cereal crop patches had a positive impact on the scaled mass index of adult female barn owls (SMI; adult female body condition), resulting in barn owls with higher SMI. Next, large barn owl brood sizes were significantly predicted by female barn owls with higher SMI in cereal crop fields with higher perimeter:area ratio (habitat complexity). However, the SMI of female barn owls along with the landscape composition metrics of cereal crops, did not significantly predict the average body mass of barn owl nestlings. These results suggest that the current landscape composition of cereal crops, characterised by low habitat complexity (low perimeter:area ratio), compromises the body condition of female barn owls and their productivity, but not the body mass of nestlings. Future conservation strategies should recommend extended perimeters of cereal crop fields to further increase barn owl numbers.

Keywords

Perimeter:area ratio; scaled mass index; brood size; body mass; barn owl nestling

3.2 Introduction

Several studies have shown a strong positive relationship between food availability, maternal body condition and consequent reproductive productivity (Sumasgutner *et al.*, 2014; Navarro-López, Vergara and Fargallo, 2014; Podofillini *et al.*, 2019). For example, higher breeding densities in the Eurasian Kestrels (*Falco tinnunculus*) in Vienna were associated with suitable nest cavities in urban areas but their reproductive productivity was compromised by the lack of food resources, resulting in nest desertion, lower hatching rates and smaller-fledged broods (Sumasgutner *et al.*, 2014). While Navrro- López, Vergara and Fargallo (2014) showed that kestrels with higher body condition fed their nestlings with larger amount of diverse prey species that was positively associated with higher body condition and stronger immune response in kestrel nestlings. Similarly, Podofillini *et al.* (2019) showed that extra food provisioned for brooding of lesser kestrel (*Falco naumanni*) females was allocated to produce heavier eggs, improve early nestling growth, and lower the negative effects of ectoparasites on nestling body mass. In sum, these examples demonstrate that greater food availability can positively impact female body condition of raptors, improving the chances of reproductive success without compromising nestling body mass and ultimately increasing the chances of survival of both the adults and the nestlings (Wiens, Noon and Reynolds, 2006; Nägeli *et al.*, 2022; Snyder and Smallwood, 2023).

Barn owl reproduction is influenced by many factors that include climate (Chausson *et al.*, 2014), mass gain prior to egg laying, and male provisioning while brooding (Durant, Gendner and Handrich, 2010). Previously, it was thought that land use and landscape composition had a direct impact on the reproductive performance of the barn owl, such that the brood size, egg laying date and probability of double brooding were negatively associated with certain landscape variables, including habitat area (Shawyer, 1998; Bond *et al.*, 2005; Meek *et al.*, 2009; Frey *et al*., 2011). For example, Shawyer (1998) found that barn owls declined in numbers when the rough grassland area around nest sites dropped below ~9ha, while an abundant presence of certain land use types such as improved grassland, suburban land and wetlands, resulted in unsuccessful barn owl nesting attempts (Bond *et al.*, 2005). In studies by Shawyer (1998) and Bond *et al*. (2005), the decline in barn owl numbers were associated with a decline in prey numbers.

In the United Kingdom, nearly 52% of the agricultural land use is comprised of cereal crops, the most dominant crop type (Department for Environment, Food and Rural Affairs, 2019). Previous studies have shown that arthropod and arachnid biodiversity (Batáry *et al.*, 2012), and small mammal abundance (primary food source of barn owls; Meek *et al.*, 2012) are negatively impacted by increasing the total area of cereal crop fields (Heroldová *et al.*, 2007). Furthermore, chapter 2 showed that larger total area of cereal crop fields had a significant negative impact on the brood size of barn owls. What remains to be studied is whether the landscape composition of cereal crop fields, characterised by the intensity of land use, the level of fragmentation, and field complexity, has a negative impact on female barn owl body condition because of low prey abundance, such that a reduction in brood size occurs.

Barn owl parents trade-off the investment of energy into either their own survival or the production of offspring (Durant, Gendner and Handrick, 2004). For example, Roulin, Ducrest and Dijkstra (1999) found that nestling mortality was higher in larger broods than in reduced broods, resulting in a reduction in brood size when more parental effort is required to provision barn owl broods. Among female barn owls, the parental effort is mostly asymmetric during incubation and brooding, wherein they are reliant on the males to deliver food (Durant, Massemin and Handrich, 2004). Furthermore, to maximise fledging success, the female adjusts the brood size according to their mate's ability to deliver food during breeding (Durant, Gendner and Handrick, 2004). In cases where the food deliveries do not match the brood requirements, the body condition of the female barn owl, rather than the nestlings, is compromised, as female barn owls do not forage until ~15 days after the first egg has hatched, regardless of male provisioning (Durant, Gendner and Handrick, 2004). Barn owl nestlings leave the nest for the first time anywhere between 54 and 105 days, and the nestlings venture up to 4km from their nests (Roulin, 2020). The nestlings definitively leave their nests and abandon the surrounding area at around 90 days on average, and nestlings are often evicted earlier if their parents are planning to have a second clutch (Roulin, 2020). Barn owls show plasticity in their foraging strategies, such that they forage beyond their home range of ~1km^2 when the immediate habitat around their nest is not suitable (Taylor, 1994; Shawyer, 1998). Furthermore, Arlettaz *et al*. (2010) showed that Swiss barn owls chose foraging habitats based on prey accessibility rather than prey abundance, and preferred to forage in cereal crop fields over all other crop types and wildflower areas (which had a higher abundance of prey). Whether a preference to foraging in cereal dominated fields impacts the body condition of female barn owls and consequently brood size remains unknown.

In this study, I propose that the landscape structure of cereal dominated fields impacts the body condition of female barn owls, thereby affecting brood size (brood size reduction) but without compromising the body condition of nestlings. The homogeneity in cereal dominated fields can result in lower small mammal abundance, negatively affecting female barn owl body condition and brood size, while an increase in the habitat complexity can promote small mammal abundance resulting in higher female barn owl condition and larger brood sizes, without compromising the body condition of nestlings. The results of this study can aid in the implementation of conservation policies to protect not only barn owls but other farmland bird species.

3.3 Materials and methods

3.3.1 Barn owl breeding data

Barn owl breeding data from the British Trust for Ornithology (BTO) comprised a total of 126 breeding records from 86 nest boxes monitored between 2016 and 2018. The data originated from the eastern part of Great Britain (East Midands and the South East), where agricultural intensity is higher than in the west (see Chapter 2). Brood size of barn owls (proxy for reproductive productivity), maximum wing chord length (mm) and body mass (g) of female adult barn owls (used to calculate scaled mass index, a proxy for body condition), and average body mass (g) of nestlings (proxy for body condition of nestlings) were obtained from each nest box (N = 126). A total of 23 cases of double-brooding were observed. To calculate the body condition of adult female barn owls, a scaled mass index (SMI) was used because it accounts for the structural size of the bird and is, therefore, a reliable indicator of fat content, necessary for both maintenance of life and reproduction (Peig and Green, 2009):

$$SMI = M_i \left(\frac{L_0}{L_i}\right)^b$$

M_i and L_i are the body mass and wing chord length, respectively, of the barn owl individual 'i'. L_0 is the mean value of the wing chord length of the sample population, and b is the slope of the reduced major axis regression of log-transformed mass on log-transformed wing chord length. SMI could not be calculated for barn owl nestlings because of the lack of wing chord length data.

3.3.2 Geospatial data on cereal crop land use and landscape structure

Geospatial data on crop cover for Great Britain published by the Centre for Ecology and Hydrology (CEH Land Cover® Plus: Crops, 2016; 2017; 2018) were used to predict the brood size and average body mass of barn owl nestlings along with SMI. The crop cover data classified cereal crops into winter wheat, spring wheat, winter barley, spring barley and maize, but were grouped to form one major category of 'cereal crops' (see Chapter 2).

To define the landscape composition of cereal crops, three landscape composition metrics were considered, namely total area (proxy for land use), number of patches (proxy for habitat fragmentation), and perimeter:area ratio (proxy for habitat complexity). The definitions, extraction procedures and use of these proxies in the literature is detailed under the materials and methods section in Chapter 2. All GIS analyses were carried out using the landscape ecology statistics plugin (LecoS; Jung, 2016) for QGIS v2.18.0 (QGIS Development Team, 2009).

3.3.3 Statistical analyses

To determine the impact of the landscape composition metrics of cereal crops (predictors: total area, number of patches and perimeter:area ratio) on adult female barn owl SMI (response variable: non-normal distribution, Shapiro-Wilk's test: $W = 0.98$, $P = 0.046$), a generalised linear mixed model (GLMM) was constructed with Gamma distribution and log link function (lme4 R package; Bates et al., 2015). Next, to determine the impact of adult female barn owl SMI (predictor 1) and the landscape composition metrics of cereal crops (predictor 2) on barn owl brood size (response variable), a GLMM was constructed with a Conway-Maxwell Poisson (CMP) distribution and loglambda link function. Adult female barn owl SMI was also included as an interaction effect with each landscape composition metric (glmmTMB R package; Brooks et al., 2017). The CMP distribution was used to deal with the under dispersion of the brood size (Shmueli *et al*., 2005; Sellers and Shmueli, 2010). Finally, to determine the impact of adult female barn owl SMI (predictor 1) and the landscape composition metrics of cereal crops (predictor 2)on the average body mass of barn owl nestlings (response variable: non-normal distribution, Shapiro-Wilk's test: $W = 0.93$, $P < 0.001$), a GLMM was constructed with a Gamma distribution and log link function. The year of nest use between 2016 – 2018 was included as a random effect for all the above three models. Model dredging procedure based on corrected Akaike information criteria (AIC_c) was not undertaken as dredging can result in spurious results of no biological significance (Smith, 2002; Burnham and Anderson, 2002). Instead, the model coefficients and corresponding confidence intervals were used to verify the predictive power of the GLMMs through simulations. A total of 10,000 barn owl brood sizes of the most commonly occurring brood size in the dataset were simulated, and compared with the actual percent of occurrence of the most common brood size in the dataset (Zuur and Ieno, 2016). Simulations were only carried out if at least one of the terms in the barn owl brood size GLMM was significant.

Landscape composition metrics are correlated to a certain extent, and the introduction of interaction effects in models tend to increase the variance inflation factor (VIF) of predictors (Robinson and Schumacker, 2009). Therefore, VIF of individual effects were verified to be <10 for all models (see example - Ohashi et al., 2020). Finally, the residual plots were visually assessed for similar variance across treatments and the impact of influential outliers for all GLMMs was carried out using the DHARMa R package (Hartig, 2022). Influential outliers with Cook's distance greater than one were removed from the analysis. All data analyses were carried out using R v3.6.2 (R Core Team, 2019).

3.4 Results

The mean scaled mass index (SMI) of adult female barn owls was found to be 340.01 ± 44.09 (mean ± SD). An increase in the number of cereal crop patches had a positive impact on the SMI of adult female barn owls, resulting in barn owls with higher SMI ($\beta = 0.006$, $CI_{95\%} = 0.0005, 0.013$; $t = 2.13$, $P = 0.033$; Fig. 3.1). However, the perimeter:area ratio and the total area of cereal crops did not have a significant impact on the SMI of adult female barn owls (Table 3.1). The model variance of the SMI of adult female barn owls explained by the random effect - year was very low; the interclass-correlation coefficient was 0.019, conditional R^2 was 0.046 and the marginal R^2 was 0.027.

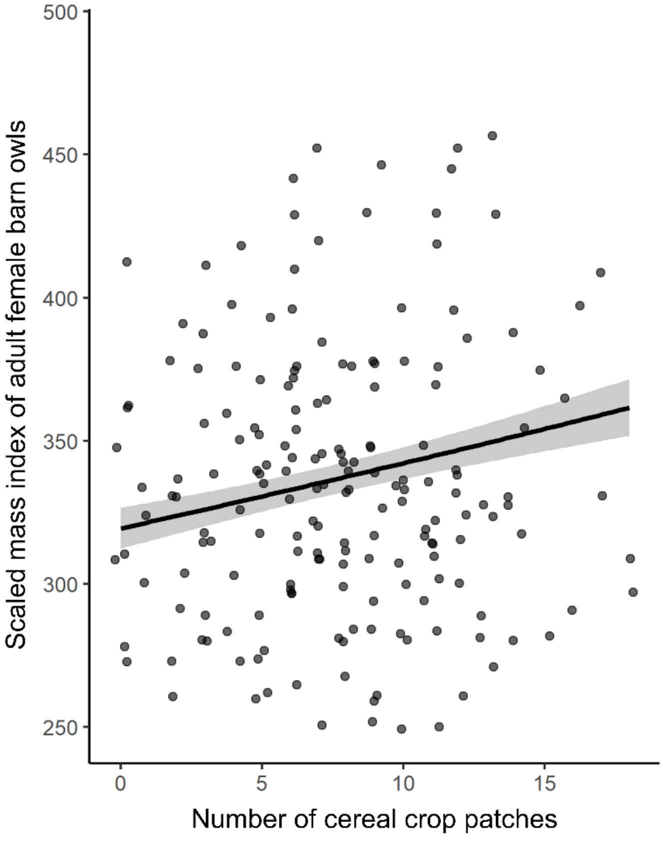

Figure 3. 1. Generalised linear mixed model with Gamma distribution and log link function, showing the relationship between the number of cereal crop patches and the scaled mass index (SMI) of adult female barn owls. An increase in the number of cereal crop patches contributed to adult female barn owls with higher SMI. Shaded areas represent 95% confidence intervals.

Next, the SMI of adult female barn owls did not have a significant effect on the brood size of barn owls by itself ($\beta = -0.003$, $CI_{95\%} = -0.008, 0.001$; $t = 0.209$, $P = 0.834$). However, when SMI was included as an interaction effect with the

Table 3.1. (a) Generalised linear mixed model with Gamma distribution and log link function predicting the scaled mass index (SMI) of adult female barn owls. (b) Generalised linear mixed model with Conway-Maxwell Poisson distribution and loglambda link function predicting barn owl brood size, and a generalised linear model with Gamma distribution and log link function predicting the average body mass of barn owl nestlings using the SMI of adult female barn owls and the landscape composition metrics of cereal crops as predictors. The individual effects of number of patches, perimeter:area ratio and total area are presented in the row corresponding to the intercept. The individual effect of SMI is presented in the intercept column, and the interactions of SMI with landscape composition metrics of cereal crops are presented in rows corresponding to the SMI. $CI_{95\%}$ – 95% Confidence intervals are provided within parentheses and significant terms are in bold. ICC – Intraclass correlation coefficient, R^2 (Cond.) – R^2 Conditional, R^2 (Marg.) – R^2 Marginal.

a)

Model	Predictors	Estimate ($CI_{95\%}$)	Random effect - year		
			ICC	R^2 (Cond.)	R^2 (Marg.)
Scaled mass index of adult female barn owls (SMI)	Intercept	5.84 (5.755, 5.93)	0.019	0.046	0.027
	Total area (ha)	-0.0002 (-0.0007, 0.0001)			
	Number of patches	**0.006 (0.0005, 0.013)**			
	Perimeter:area ratio	-2.97 (-6.726, 0.771)			

b)

Model	Predictors	Intercept	Total area (ha)	Number of patches	Perimeter:area ratio	Random effect - year		
						ICC	R^2 (Cond.)	R^2 (Marg.)
Brood size	Intercept	2.4 (0.603; 4.2)	-0.01 (-0.024; 0.001)	0.16 (-0.00003, 0.337)	-115.28 (-203.32, -272.53)	0.012	0.064	0.053
	SMI	-0.003 (-0.008; 0.001)	0.00002 (-0.000008, 0.00006)	-0.0004 (-0.0009, 0.00006)	**0.31 (0.049, 0.576)**			
Average body mass of barn owl nestlings	Intercept	5.65 (4.483, 6.82)	-0.0003 (-0.007, 0.007)	0.02 (-0.07, 0.126)	1.42 (-51.831, 54.681)	0.05	0.078	0.03
	SMI	0.0003 (-0.003, 0.003)	0.000006 (-0.00002, 0.00002)	-0.00005 (-0.0003, 0.0002)	-0.008 (-0.168, 0.15)			

perimeter:area ratio of cereal crop fields, a significant positive impact on barn owl brood sizes was observed ($\beta = 0.31$, $CI_{95\%} = 0.049, 0.576$; $t = 2.01$, $P = 0.045$). Large barn owl brood sizes were significantly predicted by female barn owls with higher SMI in cereal crop fields with higher perimeter:area ratio (habitat complexity; Fig 3.2). The total area, number of patches, total area x SMI, and number of patches x SMI of cereal crops had no significant impact on the brood size of barn owls (Table

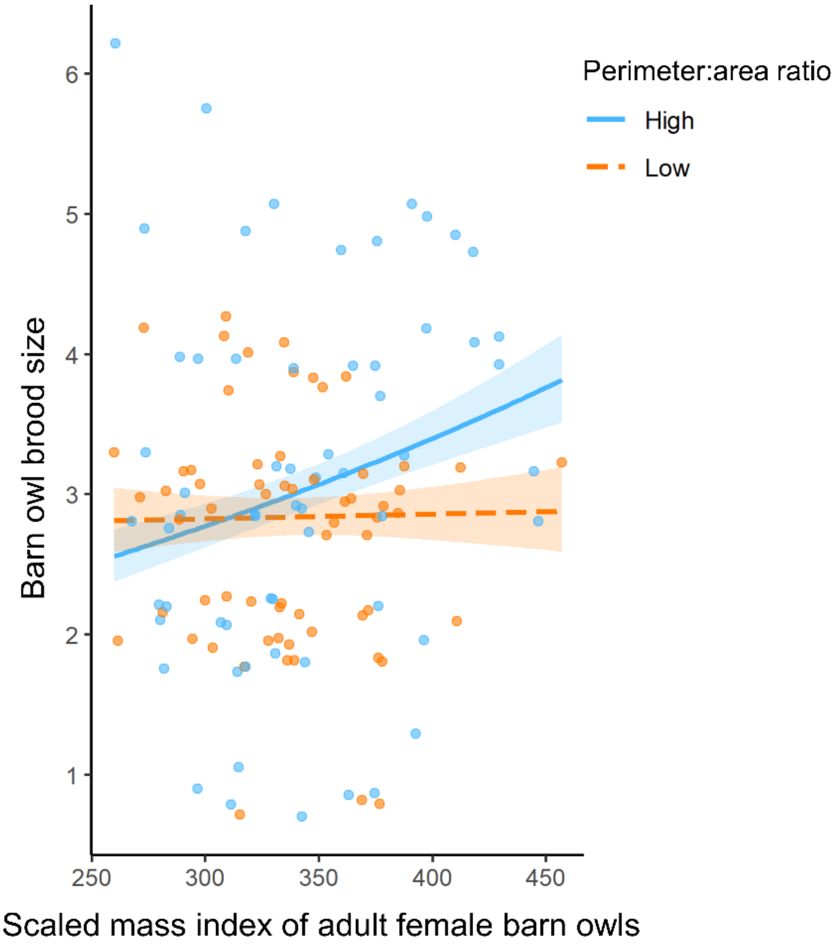

Figure 3. 2. Generalised linear mixed model with Conway – Maxwell Poisson distribution and loglambda link function, showing the relationship between the interaction of perimeter:area ratio and scaled mass index (SMI) of adult female barn owls in predicting barn owl brood sizes. Large barn owl brood sizes were significantly predicted by female barn owls with higher SMI in cereal crop fields with higher perimeter:area ratio. Perimeter:area ratio of cereal crops was grouped into high and low categories using the median as the measure of central tendency. Shaded areas represent 95% confidence intervals.

3.1). Furthermore, the average body mass of barn owl nestlings was not significantly predicted by SMI, any of the landscape structure metrics for cereal crop fields, or by the interaction of SMI with any of the landscape structure metrics for cereal crop fields (Table 3.1).

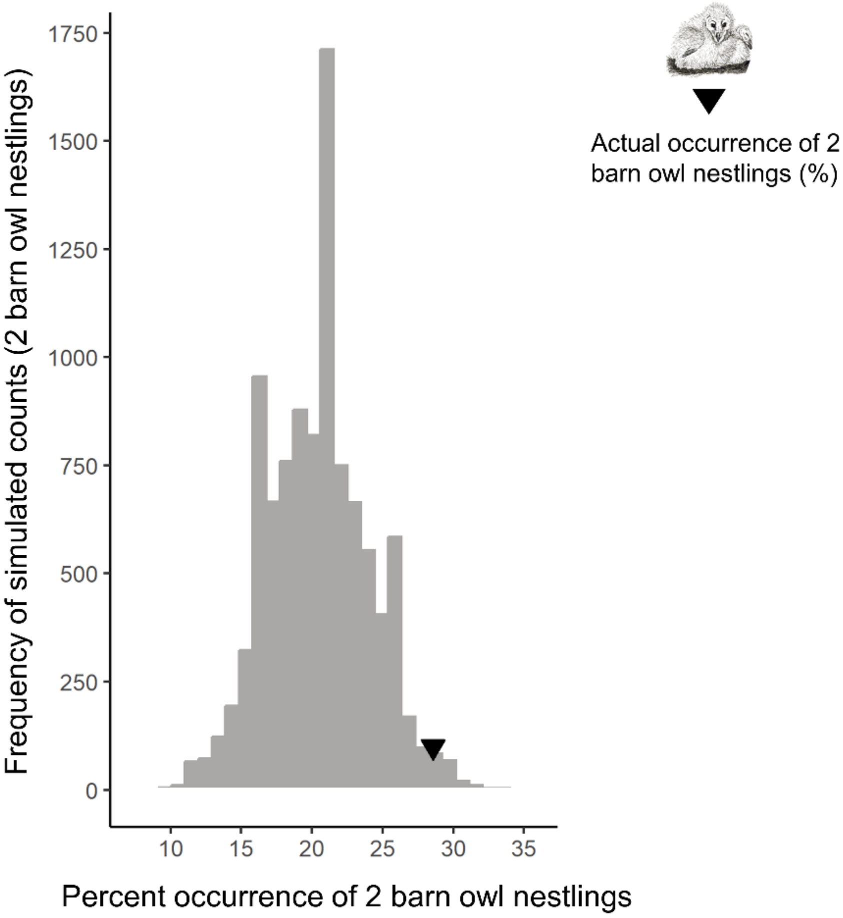

Figure 3. 3. Histogram showing the occurrence of simulated brood size of two barn owl nestlings using the Conway – Maxwell Poisson distribution GLMM model predicting brood size in relation to the individual effects of scaled mass index (SMI), number of patches, perimeter:area ratio, and total area of cereal crops, and in relation to the interaction effects of SMI with the landscape composition metrics.

The most frequently observed brood size was two barn owl nestlings per nest box. The percent occurrence of a simulated brood size of two barn owls (n = 10,000) ranged from 9 to 34% when using the CMP GLMM model. The actual percent occurrence of a brood size of two barn owls in the dataset was 28% (n=126), which is within the simulated range (9-34%), affirming the accuracy and predictive strength of the CMP GLMM (Fig. 3.3). Therefore, the combination of body condition of female barn owls, measured using SMI, and the habitat complexity metric of cereal crop fields, is a better predictor of barn owl brood size than any other agricultural landscape composition metric alone (see Chapter 2).

3.5 Discussion

Land use and landscape composition metrics by themselves are insufficient determinants of barn owl productivity (see Chapter 2). In this study, the reproductive capability of barn owls in a cereal crop dominated agricultural landscape was analysed by using the body condition of breeding adult female barn owls post egg-hatching. First, it was found that a greater number of cereal crop patches (habitat heterogeneity) had a positive impact on adult female barn owl scaled mass index (SMI), resulting in barn owls with higher SMI. Next, it was found that the SMI of adult female barn owls by itself was a poor indicator of barn owl brood size. However, when the SMI of adult female barn owls was coupled with high perimeter:area ratio (high habitat complexity) of cereal crops, a significant positive impact on barn owl brood size was observed. Large barn owl brood sizes were predicted by adult female barn owls with higher SMI in cereal crop fields with higher perimeter:area ratio. Therefore, more complex, and heterogenous cereal crop landscapes are associated with better female body condition that, in turn, contributes to larger barn owl brood sizes.

Small mammal abundance, a reliable food source for barn owls (Butet *et al.*, 2006; Gelling *et al.*, 2007), is shown to be the lowest in cereal crop fields compared to permanent habitats such as windbreaks, small woods, and fallow land (Herldová *et al*., 2007). Despite a lower abundance of small mammal abundance in cereal crop fields, barn owls are shown to preferentially forage in cereal crop fields over other crop types, mainly because of prey accessibility over prey abundance (Arlettaz *et al.,* 2010). A greater number of cereal crop patches can act as a food sink for small mammal populations (Abt and Bock, 1998) whereas the adjoining source habitats such as hedgerows and grass margins serve as vital breeding grounds to maintain small mammal populations (Boone and Tinklin, 1988). Therefore, it is likely that a greater number of cereal crop patches has a positive impact on the SMI of adult female barn owls, resulting in barn owls with higher SMI.

Barn owls determine clutch size using cues such as male food provisioning (Durant, Gendner and Handrich, 2010), and when barn owl broods require extra parental effort, a reduction in brood size occurs to ensure the survival of nestlings (Roulin, Ducrest and Dijkstra, 1999). Since barn owls adjust their reproductive capability depending on parental effort in food provisioning, barn owl brood size was not significantly predicted by the SMI of adult female barn owls alone. However, larger brood sizes were predicted by adult female barn owls with higher SMI when coupled with cereal crop fields with higher perimeter:area ratio (greater habitat complexity). Cereal crop fields with higher perimeter:area ratio can correspond to a greater availability of source habitats such as hedgerows and grass margins, which are vital breeding grounds to maintain small mammal populations, the dominant prey of barn owls (Boone and Tinklin, 1988). Furthermore, under Agro-Environment Schemes and Environmental Stewardship Schemes, farmers are encouraged to create small-mammal friendly features such as log piles, hedgerows, and grass margins, to provide essential cover and nesting sites for small mammals (Broughton *et al.*, 2014). Small mammal biomass is also shown to increase with an increase habitat complexity (Gelling et al., 2007), benefitting the body mass of predators such as barn owls. Therefore, more complex cereal crop fields are associated with better adult female barn owl body condition that, in turn, contributes to larger brood sizes.

To test the predictive ability of barn owl brood size by the combination of the SMI of adult female barn owls and the perimeter:area ratio of cereal crop fields, simulations were carried out using the model coefficients of the brood size GLMM. Brood size model simulation showed that the simulated percent occurrence range of the most commonly occurring barn owl size (two barn owls), lay within the percent actual occurrence in the dataset, suggesting that the combination of the SMI of adult female barn owls and the perimeter:area ratio of cereal crop fields are reliable indicators of barn owl brood size in agricultural landscapes.

Neither body condition nor any of the landscape composition metrics of cereal crop fields (and the interaction of body condition with the landscape composition metrics), significantly predicted the average body mass of barn owl nestlings. Small brood sizes in barn owls are a result of a lack of food resources (Roulin, 2020). For example, Roulin, Ducrest and Dijkstra (1999) have shown that when barn owl broods require extra parental effort to provision the brood, a reduction in brood size occurs with an increase in the average body mass of barn owl nestlings, to ensure their survival. Furthermore, the authors have also reported brood reduction through cannibalism to ensure survival (Roulin, Ducrest and Dijkstra, 1999). Therefore, the findings from the current study suggest that the landscape composition of cereal crops can compromise the body condition of breeding barn owls and their productivity, but not the body condition of barn owl nestlings. A better body condition of raptor nestlings can ensure survival to adulthood as it reduces the negative impact of ectoparasites (Podofillini *et al.*, 2019) and strengthens the immune system (Navarro-López, Vergara and Fargallo, 2014).

Lastly, it is important to note that barn owl brood sizes and average body mass of barn owl nestlings are not solely influenced by the relationship between maternal body condition and land use and landscape structure. For example, Chausson *et al.* (2014) found that heavy rainfall 4 – 2 weeks preceding egg laying had a positive effect on barn owl clutch size, while fledging body mass was negatively impacted by heavy rainfall 24 hours prior to taking measurements. Similarly, Almasi *et al.* (2015) found that nestlings in intensely cultivated fields had increased baseline corticosterone levels, indicating stress, contributing to lower body mass. While the findings of this study suggests that a decrease in the habitat complexity of cereal crop dominated fields can negatively impact the body condition of adult female barn owls resulting in smaller brood sizes, anthropogenic activity associated with agriculture and elements of weather can also bear a negative consequence on barn owl reproductive success.

In this study, maternal body condition and the habitat complexity of cereal crops, which happens to be the most dominant crop type in Great Britain, were the only factors that determined barn owl reproductive productivity. Findings showed that large brood sizes were predicted by adult female barn owls with higher SMI in cereal crop fields with higher perimeter:area ratio. Previous studies have linked habitat complexity to prey abundance (August, 1983; Boone and Tinklin, 1988; Roberts *et al*., 2008). Future studies should investigate the impact of food availability and male barn owl foraging strategies, specifically male food provisioning in cereal-dominated landscapes, to thoroughly understand the determinants of maternal barn owl body condition during the breeding season, and brood sizes. Most importantly, this study highlights the need for a scale-dependent framework in organismal biology to understand the reproductive ecology of a species, wherein positive or negative effects on a life-history trait (such as in reproduction or foraging) can be generated by the immediate environment and demands in energetic needs (Agrawal, 2020). It is recommended that future barn owl and other raptor studies undertake a holistic approach and accommodate the vital determinants of reproductive biology that can enhance the implementation of conservation measures for farmland raptors.

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Chapter 4

Indirect effects of pesticides on barn owl breeding in Great Britain

4.1 Abstract

Raptors are a natural alternative to pesticides as they aid in controlling various vertebrate pest species through prey consumption. The current use of pesticides is detrimental to farmland biodiversity, impacting the whole food chain including species at higher trophic levels such as raptors. One such species, the barn owl, can hypothetically be impacted by broad spectrum pesticides as this has knock-on effects on barn owl prey, small mammals, so can negatively impact barn owl reproduction. In this study, the indirect effects of fungicides (chlorothalonil) and herbicides (diflufenican, flufenacet and glyphosate) used in cereal production are used to predict barn owl brood sizes (a proxy for reproductive performance) and body mass of nestlings (a proxy for nestling body condition). Generalised linear mixed models were used to predict barn owl brood size and body mass of nestlings between three regions of Great Britain that differ in the intensity of agriculture and pesticide use (Midlands, South East and South West). First, the total use of chlorothalonil, diflufenican and flufenacet was found to be the highest in the Midlands, followed by the South East and South West of Great Britain, whilst glyphosate use did not differ between the Midlands and the South East, but was significantly lower in the South West of Great Britain. Second, neither chlorothalonil, diflufenican or glyphosate significantly predicted barn owl brood size or body mass of nestlings. Flufenacet, a herbicide moderately toxic to birds and mammals, had a significantly negative impact on barn owl brood size, but not nestling body mass, irrespective of region. An increased use of flufenacet had a negative impact on barn owl brood size, accurately predicting small brood sizes. Overall, it is likely that flufenacet use in the production of cereals, the most dominant crop type in Great Britain, is restricting barn owl productivity. Consequently, the future use of flufenacet as a pesticide must be reconsidered in the implementation of integrated pest management schemes in the UK.

Keywords

Flufenacet; body mass; nestlings; brood size; cereal; agriculture.

4.2 Introduction

Pesticides are chemical or biological agents used widely to protect crops and increase yields, by controlling pests and weeds (Abubakar *et al.*, 2020). The use of pesticides is shown to reduce crop losses by 40%, making their use economically and socially justifiable (Richardson, 1988). One of the earliest pieces of evidence of pesticide use dates back to the 1500's where mercury and arsenic were used as insecticides (Abubakar *et al.*, 2020). Later, in the 1940's, dichloro-diphenyl-trichloroethane (DDT), an insecticide, was discovered, marking the advent of the synthetic pesticide era that could not only prevent damage to crops efficiently but also decrease the transmission rate of diseases such as malaria (Beard, 2006). However, the use of DDT soon came to an end around the 1960's because of the harmful effects noted in non-target organisms that were elaborated on in the book "Silent Spring" by Rachel Carson (Carson, 1963). For example, the metabolites of DDT (DDE) are lipid-soluble compounds that persist in the food chain and bioaccumulate in the fat tissues of the human body, leading to increased risk of occurrence of various types of cancer (Jaga and Brosius, 1999). Similarly, the use of DDT had a detrimental impact on raptors, causing eggshell thinning, resulting in cracked eggs and increased egg destruction, often accidentally, by parents (Porter and Wiemeyer, 1969; Olsen, Fuller and Marples, 1993; Hartley and Douthwaite, 1994; Falk *et al*. 2018). Even with many countries around the world banning the use of DDT in the early 1970's, the long-lasting effects of DDT are still evident among raptors, where eggshell thickness has now increased but not to the extent it was pre-DDT use (Falk *et al*. 2018). Consequently, Falk *et al.* (2018) predict that Greenlandic peregrines (*Falco peregrinus*) will not have normal eggshells (pre-DDT use eggshell thickness) until 2034. Since the 1970's, DDT has been replaced with organophosphate and carbamate pesticides which pose a lower risk to humans and non-target organisms, and are still in use today (Abubakar *et al.*, 2020). Furthermore, Environmental Risk Assessments (ERA) were introduced in 1991 by the European Union (EU) as a procedure for candidate pesticides to be approved and registered under the 91/41/EEC Council Directive prior to use in agriculture (European Parliament, 2009).

Since the introduction of ERAs in the EU, the pesticide legislation has safeguarded human quality of life and that of non-target organisms by banning the use of pesticides that were formerly authorised (e.g. ethoprophos, thiamethoxam, dichlorvos, etc.). This is because of unexpected and unacceptable risks to human safety (e.g. cancer causing), non-target organisms and the environment, that emerged after their initial introduction to the market (Storck *et al*., 2017). At present, an estimated 800 active ingredients of pesticides are available for use world-wide, and since the introduction of the ERA, 2.53 million metric tons of pesticides containing these active ingredients have been used globally between 1991 and 2001 (Finizio and Villa, 2002). In the United Kingdom, a total of 44 million hectares of land were treated in the 1990's compared to a 63% increase to 73 million hectares in 2016 (Food and Environment Research Agency, 2017). Furthermore, the UK saw a dramatic increase in the weight of pesticides applied to arable crops between 2010 (14.2 tonnes) and 2016 (16.7 tonnes) by 2.5 thousand tonnes, while the overall changes in area of arable crops grown has been constant at approximately 4000 hectares between 2010 and 2016 (Food and Environment Research Agency, 2017). Among the arable crops grown in the UK, a dominant 44% comprises of cereals and is treated with nearly 9000 tonnes of pesticides, 75% of which are fungicides and herbicides (Food and Environment Research Agency, 2017). Regular application of pesticides results in a loss of plant biodiversity that then reduces associated arthropod communities, negatively impacting species that are higher up the food chain. Therefore, birds, small mammals and amphibians, are indirectly affected by pesticide use because of the causal lack of food resources (Sullivan *et al*. 1998; Mitra, Chatterjee and Mandal, 2011; Brühl *et al.* 2013). In apex predators like raptors, pesticide contamination occurs primarily through bioaccumulation, where pesticide residues are transferred across intermediate trophic levels in the food chain (e.g. small mammals and insects) which are reliable food sources for raptors (Ali *et al*., 2021). For example, Byholm *et al*. 2020 found neonicotinoid (insecticide) residues in the European honey buzzard (*Pernis apivorus*) through the process of bioaccumulation. Neonicotinoid contamination was correlated with the presence of oil plants within the foraging range of honey buzzards that fed nestlings with wasps and bumble bees containing neonicotinoid residues, which can have sublethal effects on buzzard health and development (Byholm *et al*. 2020). At present, exploring whether the widespread use of pesticides in the cultivation of cereal crops, the most dominant crop type in Great Britain, compromises the reproductive potential of a flagship conversation species such as the barn owl, can help improve pesticide legislation for the benefit of all farmland biodiversity.

The assessment procedures for ERAs of candidate pesticides are restricted to toxicity studies and calculations of predicted exposure values to estimate risk in non-target organisms, including humans (Storck *et al*., 2017). Consequently, a number of influential factors that determine the spread of pesticides such as vegetation structure (e.g. canopy cover), weather patterns (e.g. wet and dry season) and demographic characteristics (e.g. breeding period) of the exposed populations are lacking (Edge and Schauber, 2000; Köhler and Triebskorn, 2013). In most cases, ERAs do not address the impact of pesticide use (including the effects when multiple pesticides are applied) on trophic interactions in ecosystems (Brühl and Zaller, 2019). As a result, several studies have continued to show contamination of ecosystems across the world, despite the introduction of safeguarding measures such as ERAs which are followed globally (Hoferkamp *et al*., 2010; Stehle and Schulz, 2015; Ferrario *et al*., 2017; Silva *et al*., 2019; Brühl and Zaller, 2019). At present, what is needed are more elaborate procedures to be incorporated into the ERAs, as identifying the intensity of pesticide use is essential to understand ecosystem functioning in agriculture-dominanted landscapes (Sánchez-Bayo, 2011).

A species that has long-suffered from declining populations in the past is the barn owl (*Tyto alba*), because of the use of DDT and organochlorine pesticides in farming. For example, a study by Newton, Wyllie and Asher (2008) showed that nearly 40% of all barn owl mortalities in the arable counties of the Great Britain between 1963 and 1983 were because of organochlorine pesticides. Barn owl populations have since recovered (228% increase from 1995 to 2020; Harris *et al*., 2021) with the implementation of conservation measures such as banning organochlorine pesticides in 1977 (Newton, Wyllie and Asher, 2008), introducing hedgerow management schemes and installing artificial nest boxes for breeding (Newton, 2004). At present, barn owls have been studied to monitor the impacts of second-generation anticoagulant rodenticides (SGAR) on non-target organisms, primarily because of secondary poisoning through consumption of poisoned small mammal prey (Salim *et al.*, 2014; Walker *et al.*, 2020; Noh, Ahmad and Salim, 2023). For example, a recent report has shown that there has not been a significant change in SGAR residues found in barn owls since the implementation of the UK SGAR stewardship scheme in 2016 to deliver better practices for the use of SGARs and minimise the impact on non-target organisms (Walker *et al.*, 2020). SGAR exposure to barn owls has been associated with high degree of toxicity, resulting in haemorrhages and haematoma (Salim *et al*., 2014). Similarly, the decline in kestrel (*Falco tinnunculus*) abundance, a sympatric species with the barn owl, was associated with the presence of SGAR residues which had sub-lethal effects such as reduced body condition and weight loss (Roos *et al*., 2021). While there are studies to evidence the negative impacts of SGARs on raptors, studies examining the indirect effects of pesticides such as herbicides and fungicides on raptors are scarce. For example, Chu *et al.* (2007) found residues of the fungicide chlorothalonil in the eggshells of fish-eating ospreys (*Pandion Haliaetus*), through the process of bioaccumulation. The authors suggested that chlorothalonil residues in osprey eggs can potentially impact chick development, but this remains to be studied. Similarly, it is plausible that widespread pesticides such as herbicides and fungicides can have adverse indirect effects on barn owl breeding, such that smaller broods are produced with increased pesticide use, limiting barn owl numbers.

The aim of this study is to examine the impact of four widely used pesticides by weight; three herbicides (glyphosate, diflufenican and flufenacet) and one fungicide (chlorothalonil), used in the cultivation of cereal crops, the most dominant crop type in the UK, on barn owl brood size (a proxy of reproductive performance) and nestling body mass (proxy of nestling body condition) in Great Britain. The impact of the four pesticides on barn owl brood size and nestling body condition will be determined across three regions namely, the Midlands, the South West and the South East of Great Britain which differ in the intensity of agriculture and, consequently, in the amount of pesticide used. It is proposed that an increased use of herbicides and fungicides can either have direct or indirect impacts on barn owl reproduction such that smaller barn owl brood sizes with low nestling body mass are expected in the Midlands (high agricultural intensity) compared to the South East (intermediate agricultural intensity) and the South West (low agricultural intensity) of Great Britain. The results of this study can improve the existing stewardship scheme to incorporate better practices at monitoring the impact on non-target farmland species.

4.3 Materials and methods

4.3.1 Barn owl breeding data

Archived data from the British Trust for Ornithology (BTO) comprised a total of 928 barn owl breeding attempts from 379 unique nest boxes between 2012 – 2016.

The data was naturally clustered across three regions in Great Britain; Midlands (n = 357 breeding attempts; 118 nest boxes), South East (n = 359; 170), and South West (n = 212; 91). Barn owl brood size data was available for all 928 breeding attempts from 379 nest boxes, whereas the measures of the average body mass of barn owl nestlings per nest box were available for a subset of the nest boxes (n = 772/928; 320/379 nest boxes). The average body mass of barn owl nestlings comprised a total of 315 measures from 95 nest boxes in the Midlands, 254 measures from 137 nest boxes in the South East, and 203 measures from 88 nest boxes in the South West.

4.3.2 Geospatial data on pesticide use

Geospatial data on pesticide use published by the Centre for Ecology and Hydrology (CEH Land Cover plus®: Pesticides 2012 – 2016, Jarvis *et al*., 2019) were used to investigate whether there were causal relationships between the amount of pesticide applied and barn owl brood size, and the average body mass of barn owl nestlings. The geospatial dataset of pesticide use comprises the mean usage (kg/km^2) of 129 individual pesticides in Great Britain between 2012 – 2016, four of which are used in this study – glyphosate, chlorothalonil, diflufenican and flufenacet. The four pesticides chosen, made up nearly 75% of the pesticides used in the cultivation of cereal crops, the most dominant crop type in the UK at 52% (Food and Environment Research Agency, 2017). The geospatial dataset of pesticide use is comprised of 1 x 1km pixels with two raster bands, wherein the first raster band provides information on the mean application of the active pesticide ingredient in kg/km^2 between 2012 – 2016, and the second raster band provides information on the uncertainty of the estimated pesticide application calculated using 95%

confidence intervals (see supporting document for CEH Land Cover plus®: Pesticides 2012 – 2016).

The mean use of glyphosate, chlorothalonil, diflufenican and flufenacet was extracted by creating a buffer of 1km radius (3.14km^2) around each nest box, to represent the home range of barn owls (Bond et al., 2004; Meek et al., 2009). Similarly, the uncertainty estimates of pesticide application around a 1km radius of each nest box were extracted correspondingly. In addition, the total area of cereal crop fields within a 1km radius around each nest box was extracted from the Centre for Ecology and Hydrology crop cover dataset (CEH Land Cover® Plus: Crops, 2016). All GIS analyses were carried out using the landscape ecology statistics plugin (LecoS; Jung, 2016) for QGIS v2.18.0 (QGIS Development Team, 2009).

4.3.3 Statistical analyses

To assess the differences in pesticide application between the three regions, the mean application (kg/km^2) of chlorothalonil, diflufenican, flufenacet and glyphosate, between 2012 and 2016 were compared using Kruskal-Wallis tests accompanied by Mann-Whitney U pairwise comparisons.

The uncertainty estimates of pesticide application decreased with an increase in the application of pesticides by weight per unit area (kg/km^{2}; see supporting document for CEH Land Cover plus®: Pesticides 2012 – 2016). To standardise the measures of pesticide application, the mean application of each pesticide (kg/km^2; response) between 2012 and 2016 was corrected by undertaking linear regressions (n = 4; Table 4.1) with the corresponding uncertainty estimate (predictor). Residuals from linear regressions are widely used in ecology to correct for autocorrelation and are also shown to not generate bias in data contrary to other studies (Diniz-Filho, Bini and Hawkins, 2003; McCoy *et al*., 2006). The residuals of the measures of each pesticide application were used as predictors in generalised linear mixed models (GLMMs) to predict barn owl brood size and the average body mass of barn owl nestlings. First, a GLMM with a Conway-Maxwell Poisson distribution (CMP) and loglambda link function was constructed to determine the indirect impact of pesticide application on barn owl brood size between the three regions of Great Britain (glmmTMB R package; Brooks et al., 2017). A CMP distribution was used to deal with underdispersion of barn owl brood size (Shmueli *et al*., 2005; Sellers and Shmueli, 2010). Second, a GLMM with a Gamma distribution and log link function was constructed to determine the indirect impact of pesticide application on the average body mass of barn owl nestlings (non-normal distribution, Shapiro-Wilk's test: $W = 0.86$, $P < 0.001$) between the three regions of Great Britain (lme4 R package; Bates et al., 2015). The linear regression residuals of chlorothalonil, diflufenican, flufenacet, and glyphosate, interacting with region, were used as predictors of both barn owl brood size and the average body mass of barn owl nestlings. Year of nest use between 2012 and 2016 was used as a random effect in both models. In addition, the total area of cereal crops was included as a covariate in each model to verify that the indirect effects of pesticide applications on barn owl brood size and the average body mass of barn owl nestlings were not simply artefacts of land use (see Chapter 2). Model dredging procedure based on corrected Akaike information criteria (AIC_c) was not undertaken as dredging can result in spurious results of no biological significance

(Smith, 2002; Burnham and Anderson, 2002). Instead, to verify the predictive power of the brood size GLMM, model coefficients with the corresponding confidence intervals were used to simulate (n = 10,000) the percentage of occurrence of the most frequently observed maximum barn owl brood size in the dataset, and compared to the actual occurrence of the most frequently observed maximum brood size in the dataset (Zuur and Ieno, 2016).

The introduction of interaction effects in models tend to increase the variance inflation factor (VIF) of predictors (Robinson and Schumacker, 2009). Therefore, VIF of individual effects were verified to be <10 for both models (see example - Ohashi et al., 2020). Finally, the residual plots were visually assessed for similar variance across treatments and the impact of influential outliers for all GLMMs was carried out using the DHARMa R package (Hartig, 2022). Influential outliers with Cook's distance greater than one were removed from the analysis. All data analyses were carried out in R v3.6.2 (R Core Team, 2019).

Table 4. 1. Linear regression of the mean application of each pesticide (kg/km²; Y) with the corresponding uncertainty estimates of application (X). Regression equation is defined as Y = a + bX, where 'a' corresponds to the intercept and 'b' corresponds to the slope.

Pesticide	Regression equation (Y = a + bX)	r^2	t-value	P
Chlorothalonil	Y = 39.19 + (-20.01)(X)	0.18	9.52	<0.001
Diflufenican	Y = 2.31 + (-0.64)(X)	0.26	11.53	<0.001
Flufenacet	Y = 7.85 + (-1.46)(X)	0.21	9.96	<0.001
Glyphosate	Y = 57.06 + (-20.01)(X)	0.07	5.35	<0.001

4.4 Results

The use of chlorothalonil ($\chi^2 = 109.3$, df = 2, $P < 0.001$), diflufenican ($\chi^2 = 123.8$, df = 2, $P < 0.001$), flufenacet ($\chi^2 = 145.9$, df = 2, $P < 0.001$) and glyphosate ($\chi^2 = 90.75$, df = 2, $P < 0.001$), differed between the three regions of Great Britain. The application of chlorothalonil, diflufenican and flufenacet was significantly higher in the Midlands, followed by the South East then South West (Fig. 4.1; Table 4.2). However, glyphosate application did not differ in application between the Midlands and the South East (U = 9782; P = 0.721), but was significantly lower in the South West (U = 1498; P < 0.001). Lastly, glyphosate application in the South East was significantly higher than the South West of Great Britain (Table 4.2).

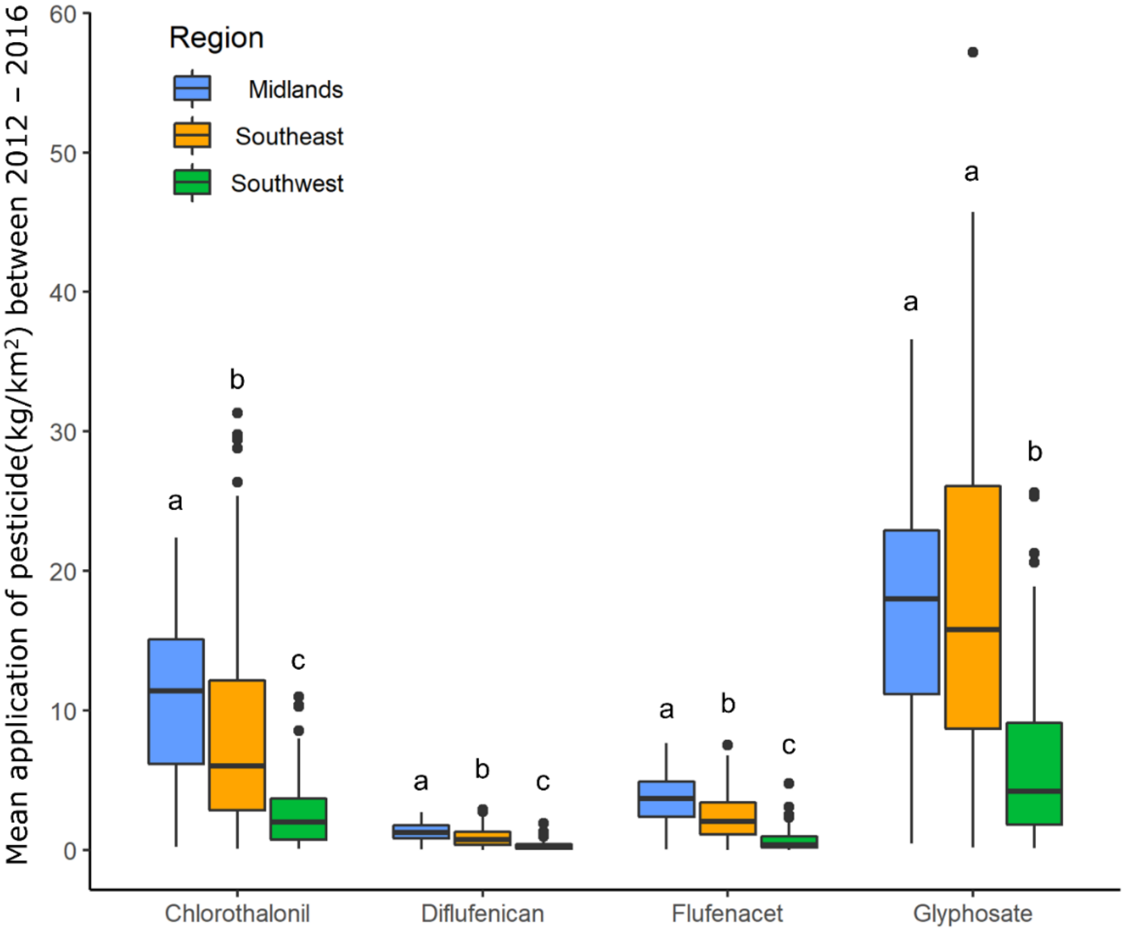

Figure 4. 5. Mean application of pesticide(kg/km²) between 2012 – 2016 for glyphosate, chlorothalonil, diflufenican and flufenacet application in the Midlands, South East and South West of Great Britain. The boxes represent the interquartile range, the bold line represents the median, the whiskers represent the minimum and maximum values and the dots represent the outliers. The lowercase letters above the boxplot represents significant differences between the three regions of Great Britain.

Table 4. 2. (a) Pairwise Mann-Whitney U tests comparing chlorothalonil, diflufenican, flufenacet and glyphosate application in cereal crop cultivation in the three geographical regions of Great Britain. Significant differences are in bold. (b) Median ± Interquartile range (IQR) of chlorothalonil, diflufenican, flufenacet and glyphosate in the Midlands, South East and South West of Great Britain. Sample sizes are provided within parentheses.

a)

Comparisons	Chlorothalonil		Diflufenican		Flufenacet		Glyphosate	
	U	P	U	P	U	P	U	P
Midlands - South East	6892	**< 0.001**	6300	**< 0.001**	5931	**< 0.001**	9782	0.721
Midlands - South West	962	**< 0.001**	839	**< 0.001**	603	**< 0.001**	1498	**< 0.001**
South East - South West	3491	**< 0.001**	3198	**< 0.001**	2591	**< 0.001**	2946	**< 0.001**

b)

Median ± IQR	Chlorothalonil	Diflufenican	Flufenacet	Glyphosate
Midlands (118)	11.38 ± 9.03	1.25 ± 0.97	3.66 ± 2.57	18.01 ± 11.94
South East (170)	6.1 ± 9.45	0.71 ± 0.93	2.04 ± 2.35	15.78 ± 17.95
South West (91)	2 ± 2.99	0.17 ± 0.34	0.35 ± 0.86	4.2 ± 7.41

Barn owl brood size differed significantly between regions and the South West had significantly larger brood sizes compared to the Midlands (pairwise contrasts based on means; t – ratio = -2.16; P = 0.045) and the South East (t – ratio = -2.91; P = 0.01) of Great Britain. Barn owl brood size did not differ significantly between the Midlands and the South East (t – ratio = 0.85; P = 0.667). Despite regional differences in barn owl brood size, flufenacet application had a significant negative impact on barn owl brood size regardless of region, resulting in smaller brood sizes (β = -0.18, $CI_{95\%}$ = -0.345,-0.028; t = -2.31, P = 0.021; Fig. 4.2). Barn owl

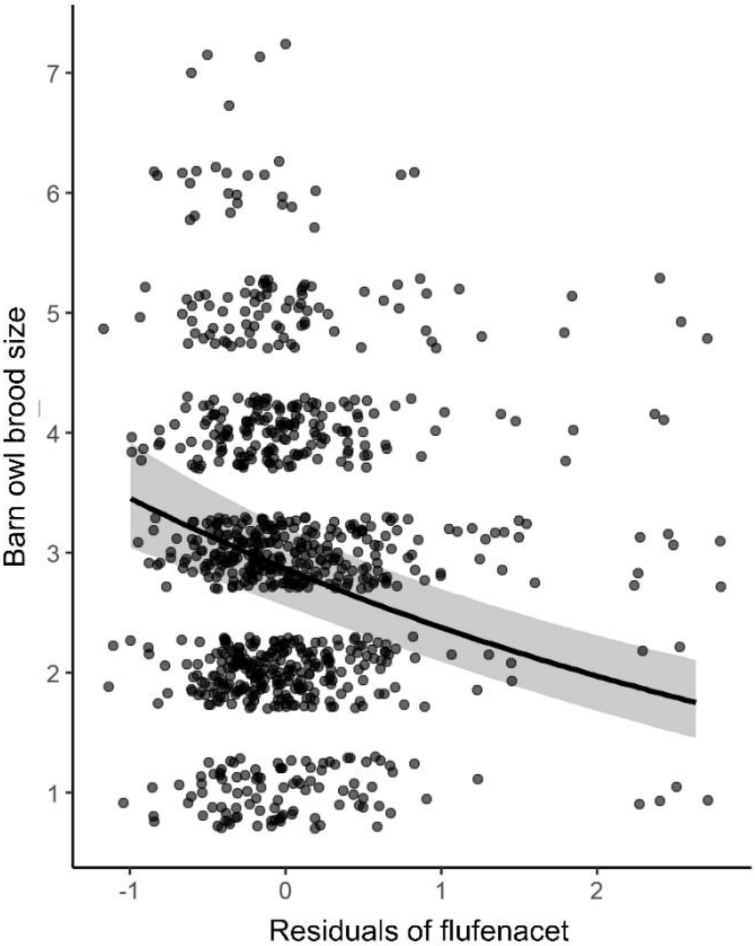

Figure 4. 6. Conway – Maxwell Poisson distribution GLMM of flufenacet pesticide, showing the relationship between flufenacet application corrected for uncertainty in application (flufenacet residuals) and barn owl brood size. Shaded areas represent 95% confidence intervals.

brood size was not significantly predicted by chlorothalonil, diflufenican and glyphosate application between regions (Table 4.3a). The model variance of barn owl brood size GLMM explained by the random effect - year was very low; the interclass-correlation coefficient was 0.059, conditional R^2 was 0.07 and the marginal R^2 was 0.012. None of the four pesticides significantly predicted the average body mass of barn owl nestlings between regions, and the model variance explained by the random effect - year was very low; the interclass-correlation coefficient was 0.015, conditional R^2 was 0.049 and the marginal R^2 was 0.034 (Table 4.3b).

The most frequently observed barn owl brood sizes were two and three barn owl nestlings per nest box. The percent occurrence of simulated brood sizes of two and three barn owls (n = 10,000 for each brood size) based on the brood size GLMM ranged from 20-29% and 1-6%, respectively (Fig. 4.3). However, the actual percent occurrence of two and three barn owl nestlings in the dataset were 27% and 31%, respectively (n = 928; Fig. 4.3). The actual percent occurrence of two barn owl nestlings lies within the simulated range of 20-29%, suggesting that the brood size GLMM is an accurate predictor of small barn owl brood sizes (Fig. 4.3). Therefore, an increased use of flufenacet in cereal crop cultivation has a significant negative impact on barn owl brood size, reducing brood sizes.

Table 4. 3. (a) Generalised linear model with Conway-Maxwell Poisson distribution and loglambda link function predicting barn owl brood size. (b) Generalised linear model with Gamma distribution and log link function predicting the average body mass of barn owl nestlings. The intercept corresponds to the Midlands, and the individual effects of region and each pesticide is presented in the row and column corresponding to the intercept. 95% Confidence intervals are provided within parentheses and significant terms are in bold. ICC – Intraclass correlation coefficient, R^2 (Cond.) – R^2 Conditional, R^2 (Marg.) – R^2 Marginal.

a) Barn owl brood size modelled with year of nest use as the random effect (ICC – 0.059; R^2 cond. – 0.07; R^2 marg. – 0.012)

Predictors	Intercept	Chlorothalonil	Diflufenican	Flufenacet	Glyphosate	Total area (ha)
Intercept	1.1 (0.948, 1.252)	0.24 (-0.32, 0.812)	0.11 (-0.137, 0.353)	**-0.18 (-0.345, -0.028)**	-0.14 (-0.547, 0.252)	-0.0005 (-0.001, -0.0001)
South East	**-0.06 (-0.122, 0.0005)**	-0.54 (-1.287, 0.201)	-0.06 (-0.347, 0.215)	0.17 (-0.002, 0.361)	0.11 (-0.37, 0.601)	
South West	0.009 (-0.067, 0.087)	-0.49 (-1.254, 0.257)	-0.007 (-0.34, 0.324)	0.23 (-0.008, 0.488)	0.19 (-0.373, 0.762)	

b) The average body mass of barn owl nestlings modelled with year of nest use as the random effect (ICC – 0.015; R^2 cond. – 0.049; R^2 marg. – 0.034)

Predictors	Intercept	Chlorothalonil	Diflufenican	Flufenacet	Glyphosate	Total area (ha)
Intercept	4.43 (4.215, 4.652)	-0.36 (-1.917, 1.182)	0.41 (-0.625, 1.447)	0.07 (-0.571, 0.719)	0.08 (-0.324, 0.485)	0.0007 (-0.0004, 0.001)
South East	0.28 (0.113, 0.453)	0.92 (-1.172, 3.02)	-0.16 (-1.472, 1.142)	0.09 (-0.681, 0.872)	-0.22 (-0.707, 0.259)	
South West	0.06 (-0.134, 0.268)	0.51 (-1.443, 2.469)	-0.506 (-1.933, 0.92)	-0.02 (-0.859, 0.811)	-0.32 (-0.952, 0.297)	

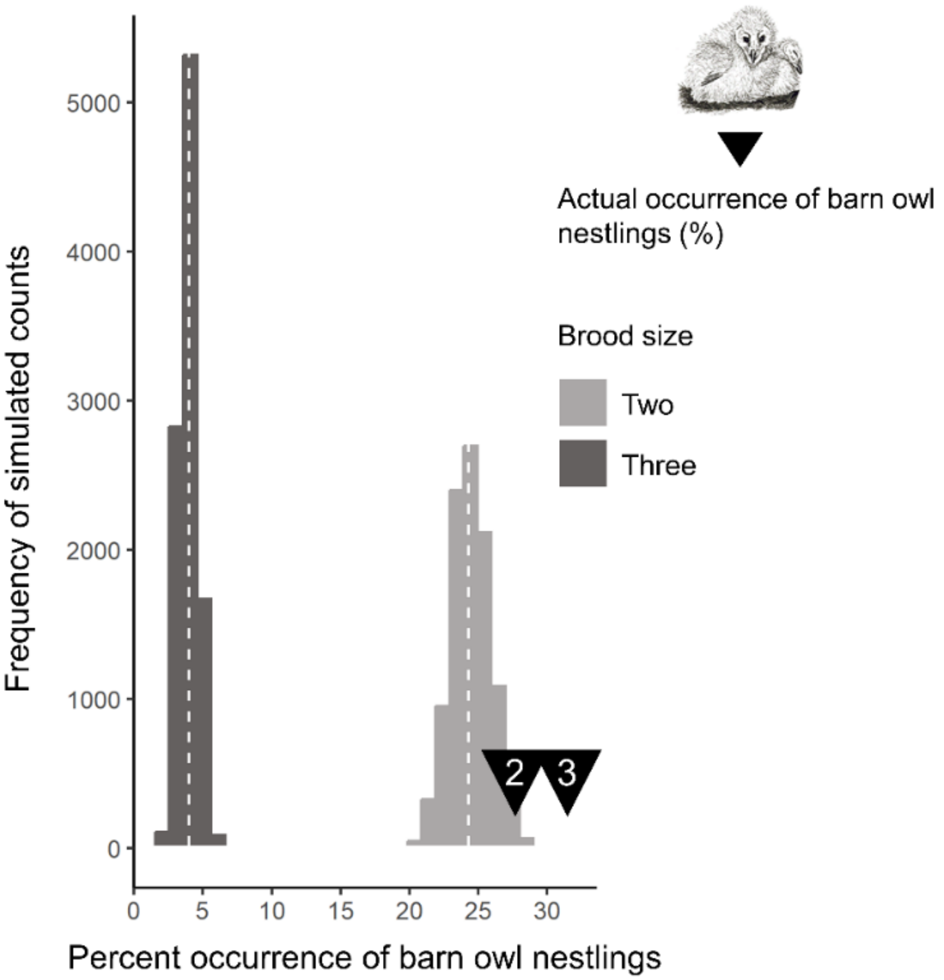

Figure 4. 7. Histogram showing the occurrence of simulated brood size of two and three barn owl nestlings using the Conway – Maxwell Poisson distribution GLMM model predicting barn owl brood size in relation to the effects of pesticide application in the cultivation of cereal crops. The dotted white lines show the maximum density of brood sizes comprising two and three barn owl nestlings.

4.5 Discussion

Global pesticide use since the early 1940s has had long-lasting harmful effects on humans, the environment and non-target organisms (Abubakar *et al.*, 2020). While the introduction of systematic procedures such as ERAs guarantees a reduction in the harmful effects of pesticides on humans and non-target organisms, ongoing research on the current use of approved pesticides on non-target organisms is lacking (Brühl and Zaller, 2019). In this first large-scale study, the indirect impacts of present-day pesticides used in the cultivation of the most dominant crop type (cereals) in Great Britain, was examined in relation to barn owl reproductive performance (barn owl brood size) and nestling body condition (average body mass of barn owl nestlings). Despite the differences in pesticide application between regions, the herbicide flufenacet had an overall negative impact on barn owl brood size, resulting in smaller barn owl broods irrespective of region. None of the pesticides significantly predicted the average body mass of barn owl nestlings.

The use of flufenacet was found to be significantly higher in the Midlands compared to the South East which ranked second, and the South West which ranked third in flufenacet usage. Even though the intensity of agriculture was the highest in the Midlands followed by the South East and then the South West (see Chapter 2), the total area of cereal crop cultivation had no significant impact on barn owl brood size, and barn owl brood size was exclusively negatively impacted by flufenacet use. The evidence for indirect effects of pesticides on avian apex predators such as raptors in the UK is limited. In Canada, it has been shown that habitat alteration with intensive use of a herbicide (glyphosate) in apple orchards adversely affected a small mammal community, reducing its populations (Sullivan *et al*. 1998). This reduction was attributed to the loss of plant food, a reliable food resource not only for small mammals but also for birds, thereby resulting in a reduction in small mammal and bird prey for raptors (Sullivan *et al*. 1998). While glyphosate, chlorothanolil and diflufenican did not significantly impact barn owl brood size or the average body mass of barn owl nestlings, residues of fungicides such as chlorothalonil have been found in the eggs of ospreys (*Pandion haliaetus*), which can impact the development of the embryo, but the impact has not been characterised (Chu *et al*., 2007). Therefore, the current trend in pesticide application can indirectly impact non-target organisms at different trophic levels, particularly apex predators such as raptors.

One of the major drawbacks with the current implementation of ERAs is the consideration of “acceptable risk” leading to the authorisation of use of candidate pesticides (Brühl and Zaller, 2019). While the authorised candidate pesticide is considered “safe” for the environment, it can still have detrimental effects on non-target species which is evidenced through continued decline in biodiversity (Brühl and Zaller, 2019). This trend of continued decline in biodiversity because of pesticide use is because ERAs target toxicity at the individual level and fail to consider the adverse effects at different trophic levels and eventually the whole ecosystem (Köhler and Triebskorn, 2013). The effects of pesticides in apex predators such as raptors are twofold such that the pesticides can have both direct and indirect effects on raptor health and survival (Ali *et al*., 2021). The direct effects include pesticide contamination in raptors as a result of bioaccumulation of pesticide residues across trophic levels through feeding has evidenced by several studies (Byholm *et al*., 2018; Dal Pizzol *et al*., 2021; Fourel, Couzi and Lattard, 2021; Badry *et al*., 2022; Noh, Ahmad and Salim, 2023). In addition, these studies have also documented secondary poisoning and other sub-lethal effects in raptors. However, the adverse direct effects of other pesticides such as herbicides and fungicides on raptor health and survival remain scarce (Ali *et al*., 2021). The indirect effects of pesticides, particularly when herbicides and fungicides are used include can include a reduction in food resources for raptors that can result in their population decline (Hole *et al*., 2005). For example, wood mice (*Apodemus sylvaticus*) utilised wheat fields that were not sprayed with any herbicides because of elevated food abundance compared to wheat fields sprayed with herbicides (Tew, Macdonald and Rands, 1992). This example suggests a trophic cascade effect where herbicides can alter the microhabitats of small mammal prey species. While the causal effect of pesticide use on small mammal prey has been established, the subsequent knock-on effects of pesticide use on raptor populations remains to be studied (Ali *et al*., 2021). Overall, it is likely that the herbicide flufenacet can either have adverse direct (e.g. secondary poisoning/sub-lethal effects) or indirect effects (e.g. lack of food resources) or both direct and indirect effects on barn owl reproduction, such that smaller brood sizes are produced with an increase in the application of flufenacet in cereal cultivation.

The ecotoxicology of every authorised pesticide is measured using the lethal dose 50 for every possible non-target organism (Lewis *et al.*, 2016). Lethal dose 50 is defined as the amount of the substance given all at once that causes death in 50% of the test animals (Ishaque and Aighewi, 2008). For example, the herbicide flufenacet is used to control certain annual grasses such as black-grass (*Alopecurus myosuroides*) and other broad-leaved weeds, has an acute oral LD_{50} of 598mg/kg in small mammals, while the acute oral LD_{50} is found to be 1608mg/kg in birds (quails), which is considered to be of moderate risk in the approval process (Lewis *et al.*, 2016). Despite flufenacet being regarded as a pesticide of moderate risk, a recent study has shown that flufenacet is responsible for developmental toxicity in vertebrates using zebrafish (*Danio rerio*) as a model system, where flufenacet adversely affected vascular and hepatopancreatic development in zebrafish (An *et al.*, 2023). Furthermore, flufenacet has also been shown to have high chronic sublethal toxicity to birds (Cech *et al.*, 2022). Therefore, it is likely that flufenacet application in the cultivation of cereal crops can have adverse direct negative impacts on barn owl brood sizes, resulting in smaller brood sizes. What remains unknown is the contamination pathway of flufenacet in barn owls, whether barn owls come into contact with flufenacet when sprayed (e.g. pesticide mist)or by consuming small mammal prey.

Barn owls are resilient raptor species with a reproductive performance dependent on the species-feeding situation, wherein the brood size of barn owls is influenced by the ability of the male to provide food (see Chapter 3). Despite the increased use of flufenacet having a significantly negative impact on barn owl brood size, the average body mass of barn owl nestlings was not affected. Simulations of the models involving flufenacet showed that a barn owl brood size of two nestlings was more accurately predicted with increased use of flufenacet compared to three barn owl nestlings, affirming the statistical reliability of the generalised linear mixed model with flufenacet as a predictor of small barn owl brood sizes. While flufenacet can reduce barn owl brood sizes, it does not impact the average body mass of barn owl nestlings. However, the data on average body mass of nestlings was collected by bird ringing groups across Great Britain, leading to possible inconsistencies in weight measures, including time of measurement and accuracy of weight measuring instruments used. Therefore, it is also likely that the data on the average body mass of barn owl nestlings is not entirely accurate and reliable enough to provide an accurate picture on the impact of flufenacet usage on the average body mass of barn owl nestlings.

Finally, the findings from this study highlight the need to incorporate procedures to tackle possible trophic cascading effects on non-target organisms and to decrease the threshold of acceptable risks to be cautious about authorisation procedures. The herbicide flufenacet was first approved in 2004 for use in the EU and its approval is set to expire in 2024 in the UK, whereas approval expired in 2021 in countries such as France and Poland (Lewis *et al.*, 2016). Future conservation measures must consider the costs and benefits of the use of flufenacet and any possible alternative herbicides. Whether flufenacet results in a decrease in small mammal abundance, thereby affecting barn owl numbers, remains unknown and must be investigated further. This study further supports the need for evidence in the field of avian ecology, that to untangle the effects of the immediate environment on life history traits such as reproduction, a wide variety of environmental stressors must be considered, allowing a better understanding of the cause-consequence effects of the environment on conservation flagship species.

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Chapter 5

Diet of breeding barn owls in cereal crop landscapes of Great Britain

5.1 Abstract

Barn owl reproduction is predominantly dependent on the provisioning of food resources by male barn owls during breeding. Infrequent provisioning of food or thereof results in lower fledging success or a failed breeding attempt. While several studies have examined the diet of the barn owl, very few have determined the impact of agricultural landscape composition of cereal crops, the most dominant crop type in Great Britain, on barn owl prey composition. In this study, a total of 322 barn owl pellets were dissected from 37 nest boxes in the Midlands (low agricultural intensity; 184 pellets) and 34 nest boxes in the South East (high agricultural intensity; 138 pellets) of Great Britain. The dietary composition of the barn owl was similar to previous studies, with the field vole (*Microtus agrestis*) being the most dominant prey type by numbers and liveweight equivalent, regardless of region (frequency of occurrence > 90%). Generalised linear models were used to predict the effects of cereal crop landscape composition on the number and diversity of small mammal prey in the diet of barn owls. An increase in the total area of cereal crops had a negative impact on barn owl prey in the South East of Great Britain, predicting a significantly lower mean number of prey items per barn owl nest box in the South East compared to the Midlands. None of the other landscape composition metrics of cereal crops significantly predicted either the mean number of prey items per barn owl nest box or the diversity of prey items per barn owl nest box. Overall, this study shows that an increase in the cultivation of cereal crops in Great Britain results in the decline of small mammal numbers such that it can restrict barn owl reproduction in the UK.

Keywords

Cereal crops; habitat complexity; crop diversity; agriculture; small mammals

5.2 Introduction

Comprising nearly 40% of the global land use, agricultural croplands and pastures have become the largest biomes on the planet (Foley *et al.*, 2005). Modern agriculture includes intensive management practices and the conversion of natural ecosystems to croplands or grazing pastures, leading to a decrease in habitat heterogeneity and the loss of diverse natural habitats (Dudley and Alexander, 2017). The decrease in habitat heterogeneity because of large-scale agriculture has resulted in the decline of species across taxa such as mammals (Put, Fahrig and Mitchell, 2019), invertebrates (Ekroos, Heliölä and Kuussaari, 2010), and birds (Chamberlain *et al.*, 2000). In particular, the decline of species in agricultural landscapes is because of the lack of food resources (Kalivodová *et al.*, 2018), unsuitable breeding habitats (Kuiper *et al.*, 2013) and mortalities associated with agricultural operations (Tews, Bert and Mineau, 2013). As a result, agriculture alters the whole environment through the transformation of natural habitats and has become a critical driver of global biodiversity loss (Dudley and Alexander, 2017).

Agriculture-driven management practices which include the clearing of non-farmed habitats such as hedgerows, grazing practices, weed control, and the spread of monocultures can alter the trophic interactions of species such as farmland birds (Boesing, Nichols and Metzger, 2017). For example, Buckingham, Peach and Fox (2006) showed that weed control and grazing intensity negatively impacted granivorous and insectivorous birds because of reduced prey abundance. Similarly, Atkinson, Buckingham and Morris (2004) showed that maintaining short swards of grass resulted in a decline in bird species that are dependent on foliar invertebrates or seeds for food. While the effects of agriculture-driven practices on lower trophic levels in agricultural landscapes can be established, however, the effects of such agriculture-driven management practices on apex predators such as farmland raptors are two-fold (Costán and Sarasola, 2021). For example, small mammals constitute the primary prey of many farmland raptors such as kestrels (*Falco tinnunculus*; Yalden and Warburton, 1979), buzzards (*Buteo buteo*; Panek and Hušek, 2014) and the barn owl (*Tyto alba*; Meek *et al.*, 2012). First, clearing of hedgerows and grazing in natural grasslands can result in a decline in small mammal prey because of the loss of cover from predators such as farmland raptors, and the lack of food resources (Gelling, Macdonald and Mathews, 2007). Second, a decrease in the abundance of small mammals can affect farmland raptor breeding success and force farmland raptors to look for alternative foraging habitats (Horváth, Bank and Horváth, 2020; Butet *et al.*, 2010). For example, Butet *et al.* (2010), showed a decrease in the abundance of the common buzzard *(Buteo buteo*) with a decrease in hedgerows and grassland areas, accompanied by a decrease in prey abundance at the landscape level in western France. However, certain crops such as oilseed rape are shown to boost small mammal populations, wherein small mammal numbers contributed to the probability of successful nesting outcomes with an increase in the number of fledglings of the common buzzard (*B. buteo*) in western Poland (Panek and Hušek, 2014). Therefore, agriculture has varying impacts on small mammal communities thereby having differential effects on farmland raptors.

Among all farmland raptors, the barn owl (*Tyto alba*) is one of the widely studied species because of its cosmopolitan distribution, with one-third of all the scientific interest invested in the diet of the barn owl because of its importance in the conservation of farmland biodiversity (Meek *et al.*, 2012; Roulin, 2020). The diet of the barn owl in the UK mainly consists of small mammals such as voles (*Microtus sp.*), wood mice (*Apodemus sylvaticus*), common shrews (*Sorex araneus*; Meek *et al.*, 2012), and occasionally reptiles (Roulin and Dubey, 2012), and has often been used to assess small mammal populations (Meek *et al.*, 2012). For example, Balestrieri *et al.* (2019) showed a sharp decline in the occurrence of shrews in the barn owl diet, which was replaced with anthropophilic rats and house mice between 1994-1995 and 2015-2016 in a protected area of northern Italy. The authors attributed these changes in the diet of the barn owl to changes in agricultural practices over the decades, indicating that agricultural practices can influence small mammal communities thereby impacting the diet of the barn owl. The reproductive success and productivity of barn owls are directly influenced by the amount of food female barn owls receive during incubation and brooding (Durant, Gendner and Handrick, 2004; Durant, Massemin and Handrich, 2004). For example, the mortality among nestlings was the highest in larger brood sizes (associated with food availability) compared to small brood sizes when extra parental effort was necessary to provide for large brood sizes (Roulin, Ducrest and Dijkstra, 1999). Therefore, there is a trade-off between the investment of energy to produce offspring and the investment of energy for their own survival among barn owls (Durant, Gendner and Handrick, 2004). The parental effort among barn owls is asymmetric where the males are responsible for delivering food to the incubating and brooding female barn owls

(Durant, Massemin and Handrich, 2004). During the breeding season, barn owl males can hunt far from their nest depending on the quality of the immediate habitat; for example, barn owls are shown to hunt as far as 4.2km in Germany, 4.5km in Scotland and anywhere between 5 and 53km in Switzerland, in one night (Roulin, 2020). Barn owls are shown to travel at around 18km/h when they are hunting and at 25km/h when delivering captured prey (Roulin, 2020). A recent study by Séchaud *et al.* (2022), showed that male barn owls foraged anywhere between 6 and 19.8km^2 depending on the quality of the nesting habitat. Males were found to feed female barn owls less frequently when they foraged further away from the nests in poor-quality habitats, resulting in a slower growth rate of nestlings that have hatched late (youngest of the brood) thereby resulting in lower fledging success (Séchaud *et al.*, 2022). Therefore, the immediate quality of the habitat around nest sites of barn owls is vital in predicting the outcome of barn owl reproductive success and productivity.

Nearly 52% of agricultural land in the United Kingdom is comprised of cereal crops, making cereals the most dominant crop type according to the Department of Environment, Food and Rural Affairs (2019). Studies from Europe have shown that cereal crops had the least abundance of small mammals such as voles (*Microtus sp.*) and wood mice (*A. sylvaticus*) in the Czech Republic (Heroldová *et al.*, 2007) whereas voles (*Microtus sp.*) and house mice (*Mus musculus*) were found to be dominant in cereal crop fields in Romania (Benedek and Sîrbu, 2018). While there is evidence that agriculture, particularly cereal crops can have differential effects on small mammal abundance and communities in mainland Europe, the effects of the agricultural landscape structure of cereal crops on small mammal abundance and communities in Great Britain remain unknown. Furthermore, Chapter 2 showed that an increase in the total area of cereal crops resulted in smaller brood sizes for barn owls, while Chapter 3 showed that the body condition of maternal barn owls improved with an increase in the habitat complexity (perimeter:area ratio) of cereal crop fields. Altogether, maternal barn owl condition and thereby productivity is negatively impacted by cereal crops in the United Kingdom. What remains to be studied is whether the negative impact of cereal crops on barn owl reproductive performance is in part because of small mammal prey composition in the diet of barn owls.

The aim of this study is to examine the small mammal composition through barn owl pellet dissections from nest boxes in the Midlands and the South East of Great Britain, as these two regions significantly differ in agricultural landscape composition (see Chapter 2), and to determine the impact of agricultural landscape composition of cereal crops on small mammal prey composition. First, to evidence the differences in agricultural landscape composition within 3.14km^2 (presumed barn owl home range, see Chapter 2) around the next boxes between the Midlands and the South East of Great Britain, landscape composition metrics such as the total area of cereal crops (a proxy for land use), number of patches of cereal crops (a proxy for habitat fragmentation) and perimeter:area ratio (a proxy for habitat complexity; see Chapter 2) were compared. Second, small mammal prey composition through barn owl pellet dissections per nest box (standardised for the number of pellets dissected) was compared between the nest sites in the Midlands and the nest sites in the South East of Great Britain. Here, I hypothesise that the region with a greater total area of cereal crops around barn owl nest boxes will result in a lower representation in both number and diversity of small mammal prey in barn owl diet. Next, I propose that a greater number of patches (increased habitat heterogeneity) and greater perimeter:area ratio (increased habitat complexity) of cereal crops will result in a higher representation in both number and diversity of small mammal prey in barn owl diet. The findings of this study will complement the findings of Chapter 2 and Chapter 3 where it is shown that the total area of cereal crop fields negatively impacts barn owl reproduction, and further facilitate in the strategic implementation of agro-environmental policies.

5.3 Materials and methods

5.3.1 Barn owl pellet collection and analysis

A total of 322 barn owl pellets (Midlands = 184; South East = 138) were collected from breeding barn owl nest boxes (Midlands = 37; South East = 34) by licensed bird ringers between July and September 2019. The barn owl pellets from the Midlands came from nest boxes located in grids SD, SJ, SK and TF, while barn owl pellets from the South East came from nest boxes located in grids TL, TM and TQ (see Appendix A).

Barn owl pellets were dissected by hand and the prey items were identified using the tooth root patterns in head parts such as the skull and the lower jaw bones, and the number of individuals was ascertained by counting the skulls or the lower jaw bones (using both the left and the right lower jaw bone to form one individual), or by a combination of both the skulls and the lower jaw bones when either the skull or the lower jaw bones were missing/broken (Lawrence and Brown, 1967). A total of 4-5 pellets were dissected on average from each nest box and the prey items were identified to the species level where possible, and unidentifiable prey was grouped together under 'Other' prey category. The 'Other' prey category also included the skulls of two unidentifiable birds recovered from pellet dissections in the Midlands. The sample sizes were deemed sufficient in the following manner: Barn owls in the UK are shown to forage as far as 4km from their nests (Shawyer, 1998). Therefore, the maximum foraging range of barn owls around each nest box with a radius of 4km was calculated to be an area of 50km^2 (area of a circle/maximum foraging range around each nest box = $\Pi \times 4^2$). All nest boxes that overlapped in the maximum foraging range of barn owls (50km^2) within and between British National Grids were grouped together based on the location of the furthest nest box in a cluster as the point of reference (see Appendix A). As a result, a total of nine 50km^2 clusters were formed (Midlands = 6; South East = 3), and the sample sizes were then deemed sufficient using species accumulation curves and the Chao 2 nonparametric estimator (Chao, 1987; Chao *et al.*, 2009) for prey items recovered through pellet dissections from each of the nine clusters (see Appendix B).

To examine the dietary composition of the barn owl, the frequency of occurrence (FO) and the percent of relative occurrence (RO) of each prey type was calculated by region (Balakrishna, Batabyal and Thaker, 2016). The frequency of occurrence of each prey type was calculated as:

$$FO = \frac{S(100)}{N}$$

where S is the number of pellets containing each prey type and N is the total number of pellets sampled. Frequency of occurrence shows the most commonly occurring prey type in the diet of the barn owl irrespective of the occurrence of other prey types. The percent of relative occurrence was calculated as:

$$RO = \frac{p(100)}{T}$$

where p is the total number of each prey item occurring in all the pellets and T is the total number of prey items from all the pellets, representing the relative importance of a given prey type in the diet of the barn owl (Loveridge and Macdonald, 2003). Next, a dietary overlap index (Pianka, 1973) was calculated to determine the degree of trophic niche overlap in the diet of barn owls between the Midlands and the South East of Great Britain. The dietary overlap was calculated as:

$$Overlap_{xy} = \frac{\sum X_i Y_i}{\sqrt{(\sum X_i^2 \sum y_i^2)}}$$

where X_i is the relative frequency of the prey type "i" in the Midlands and Y_i is the relative frequency of the prey type "i" in the South East of Great Britain. The dietary overlap values range from 0 to 1, with values closer to 1 indicating a high degree of trophic niche overlap in the diet of the two populations. Finally, the diversity of prey recovered from each nest box was calculated using Simpson's diversity index (Simpson, 1949) for each region:

$$D = 1 - \frac{\sum n(n-1)}{N(N-1)}$$

where n stands for the number of individuals of each prey type, while N stands for the total number of individuals of all prey types. The final Simpon's diversity is calculated as 1-D (dominance index), with higher measures of the diversity index indicating higher diversity and vice versa.

Finally, liveweight equivalent of barn owl prey were calculated using the average prey weights calculated by Southern (1954), Yalden and Morris (1990), and Meek *et al.* (2012). Bird and frog remains ('Others' category) were given a figure of 20g, and the average weight per species were as follows: Field vole, 21g; wood mouse, 18g; common shrew, 8g; pygmy shrew, 4g; bank vole, 16g; house mouse, 12g; brown rat, 60g.

5.3.2 Geospatial data on cereal crop land use and landscape structure

Since barn owl pellets were collected in 2019, the data on cereal crop land use in the Midlands and the South East of Great Britain was obtained from the Land Cover® Plus: Crops (2019) geospatial dataset published by the Centre for Ecology and Hydrology (CEH Land Cover® Plus: Crops, 2019). The crop cover dataset consisted of 5 cereal crop types: maize, spring barley, spring wheat, winter oats, winter barley and winter wheat. The cereal crop types were grouped into one category called 'cereal crops' based on vegetation structure and overlapping seasonal phenology (see Chapter 2).

To define the landscape composition of cereal crops in the Midlands and the South East of Great Britain, three landscape structure metrics were used, namely total area (a proxy for land use of cereal crops), the number of patches (a proxy for habitat fragmentation of cereal crop fields), and perimeter:area ratio (a proxy for habitat complexity of cereal crop fields). In addition, Simpson's diversity index was calculated for all crop types around each next box to determine the effects of crop diversity on the numbers and diversity of small mammals in the diet of barn owls. The definitions and the extraction procedures, along with the use of these proxies in literature is detailed under the materials and methods section in Chapter 2. All GIS analyses were carried out using the landscape ecology statistics plugin (LecoS; Jung, 2016) for QGIS v2.18.0 (QGIS Development Team, 2009).

5.3.3 Statistical analyses

To assess differences in the agricultural landscape composition of cereal crops, four Mann-Whitney U tests were used to compare total area, number of patches, and perimeter:area ratio, and crop diversity around barn owl nest boxes between the Midlands and the South East of Great Britain.

Next, the impact of the agricultural landscape composition of cereal crops on the mean number of prey items per nest box and the diversity of small mammal prey per nest box were determined by undertaking two generalised linear models (GLM) with Gaussian distribution and log link function (lme4 R package; Bates et al., 2015). The dependent variables, namely the mean number of prey items per barn owl nest box and the diversity of prey items per barn owl nest box, conformed with Shapiro-Wilk's tests for normality of distribution and Levene's test for homogeneity of variance by region (see Appendix C). Generalised linear mixed models with nest box cluster as a random effect could not be constructed as the models resulted in singular fit, meaning the model variance accounted by the random effect – nest cluster was zero. To model the impact of agricultural landscape composition on the mean number of prey items per barn owl nest box (model 1), the total area, number of patches, perimeter:area ratio of cereal crops and crop diversity were used as predictors with region included as an interaction effect with each landscape composition metric. Similarly, to model the impact of agricultural landscape composition on the diversity of prey items per barn owl nest box (model 2), the total area, number of patches, perimeter:area ratio of cereal crops and crop diversity were used as predictors with region included as an interaction effect with each landscape composition metric. Model dredging procedure based on corrected Akaike information criteria (AIC_c) was not undertaken as dredging can result in spurious results of no biological significance (Smith, 2002; Burnham and Anderson, 2002). The introduction of interaction effects in models tend to increase the variance inflation factor (VIF) of predictors (Robinson and Schumacker, 2009). Therefore, VIF of individual effects were verified to be <10 for both models (see example - Ohashi et al., 2020). Finally, the residual plots were visually assessed for similar variance across treatments and the impact of influential outliers for all GLMs was carried out using the DHARMa R package (Hartig, 2022). Influential outliers with Cook's distance greater than one were removed from the analysis.

Finally, to evidence the differences in the average biomass (liveweight equivalent) of barn owl prey between the Midlands and the South East of Great Britain, a Mann-Whitney U test was used. All data analyses were carried out using RStudio v3.6.2 (R core Team, 2019).

5.4 Results

Cereal crop landscape composition differed between the Midlands and the South East of Great Britain. The total area of cereal crops (U = 368, P = 0.002) and the crop diversity (U = 353, P = 0.001) around barn owl nest boxes significantly differed between the Midlands and the South East (see Table 5.1). The total area of cereal crops around barn owl next boxes was significantly greater in the South East (median ± IQR, 90.21 ± 97.39ha) compared to the Midlands (10.12 ± 86.34). Similarly, the crop diversity around barn owl nest boxes was significantly greater in the South East (median ± IQR, 0.69 ± 0.23) compared to the Midlands (0.23 ± 0.72). Finally, the number of patches (U = 466.5, P = 0.061) and the perimeter:area ratio of cereal crop fields (U = 552, P = 0.375) around barn owl nest boxes did not differ significantly between the Midlands and the South East of Great Britain (see Table 5.1).

A total of 992 prey items (Midlands = 625; South East = 367) were recovered from 322 barn pellets from the Midlands (n = 184) and the South East of Great Britain (n = 138). The sample sizes were deemed sufficient using the Chao 2 nonparametric estimator and species accumulation curves (Table 5.2; Appendix A). Field voles (*Microtus agrestis*) were the most commonly occurring prey item in the diet of barn owls in the Midlands (FO = 92.39%) and the South East of Great Britain (FO = 84.78%; Table 5.3a). However, considering all prey items recovered in the diet of the barn owls from the Midlands and the South East, the common shrew (*Sorex araneus*) was the second most dominant prey item in the Midlands (RO = 18.03%) compared to wood mice (*Apodemus sylvaticus*) in the South East (RO = 23.45%). In contrast, wood mice ranked third in the diet of barn owls in the Midlands (RO =

9.17%), compared to the common shrew in the South East (RO = 10.61%). Prey types that constituted less than 10% in both their frequency of occurrence and percent relative occurrence from both the Midlands and the South East included the pygmy shrew (*Sorex minutus*), the bank vole (*Myodes glareolus*), house mouse (*Mus musculus*) and rats (*Rattus sp.*), along with unidentifiable prey items grouped together under 'Other' prey types (see Table 5.3a). The dietary overlap of barn owl diet was found to be 0.95 (95% overlap) in the Midlands and the South East of Great Britain, indicating a high degree of trophic niche overlap in barn owl diet from both regions.

Table 5. 2. Mann-Whitney U pairwise comparisons of total area (ha), number of patches, perimeter:area ratio of cereal crops, and crop diversity (Simpson's diversity index) between the Midlands and the South East of Southern Great Britain. The number of nest boxes around which the landscape metrics were extracted is provided within parentheses for each region. All significant results are in bold.

Mann-Whitney U test pairwise comparison - Midlands vs. South East				
Landscape metrics	U	P	Median ± Interquartile range	
			Midlands (37)	South East (34)
Total area (ha)	**368**	**0.002**	10.12 ± 86.34	90.21 ± 97.39
Number of patches	466.5	0.061	2 ± 10	6 ± 5.5
Perimeter:area ratio	552	0.375	0.015 ± 0.02	0.014 ± 0.006
Crop diversity	**353**	**0.001**	0.23 ± 0.72	0.69 ± 0.23

The proportion of the liveweight equivalent of field voles was the highest in both the Midlands (64.81%) and the South East (60.23%) of Great Britain. While the rest of the prey species accounted for less than 10% of the total liveweight equivalent in the Midlands, the proportion of liveweight equivalent of wood mouse was the second highest in the South East comprising 23.38% (Table 5.3b). Overall, the mean liveweight equivalent of barn owl prey per nest box was significantly greater in the Midlands (median ± interquartile range; 61.12 ± 22.71) compared to the South East (50.5 ± 17.43) of Great Britain (U = 829; P = 0.011; Fig. 5.1).

Table 5. 2. Chao 2 nonparametric estimates of all prey species recovered from barn owl nest boxes. Observed values represent the total number of prey species recovered from barn owl nest boxes in each nest box cluster. Predicted values represent the total number of prey species that would be recovered from barn owl nest boxes given the total number of pellet dissections that have been carried out in each nest box cluster. Bootstrap values of the predicted are also provided.

Barn owl nest box clusters	Barn owl prey taxa		
	Observed	Predicted (± SD)	Bootstrap of predicted (n = 1000)
Grid SD (North)	7	7 ± 0.24	7
Grid SD (South)	6	6 ± 0.18	6
Grid SJ & SK (North)	4	4 ± 0.03	4
Grid SJ & SK (South)	5	5 ± 0.01	5
Grid TF (North)	6	6 ± 0.24	6
Grid TF (South)	6	6 ± 0.44	6
Grid TL & TM (North)	6	6 ± 0.44	6
Grid TL & TM (South)	7	7 ± 1.27	8
Grid TQ (North)	6	6 ± 0.16	6

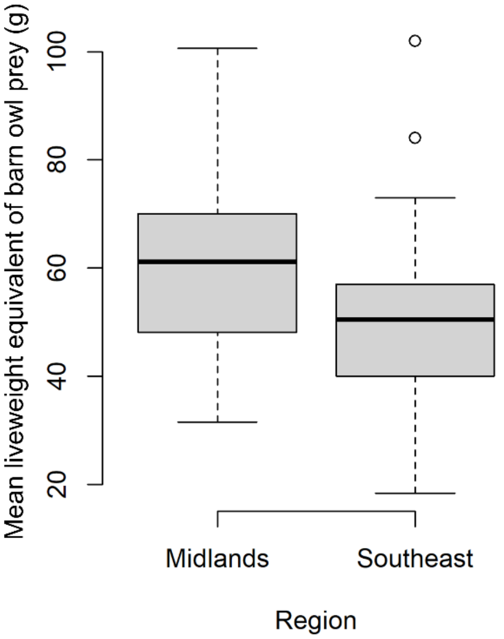

Figure 5. 8. Boxplot of mean liveweight equivalent of barn owl prey (g) in each nest box the Midlands (n = 37) and the South East (34) of Great Britain. The boxes represent the interquartile range, the bold line represents the median, the whiskers represent the minimum and maximum values and the dots represent outliers.

Table 5. 3. Absolute prey number, a) frequency of occurrence (FO%) and the percent relative occurrence (RO%), b) liveweight equivalent (g) and percent weight, of barn owl prey items recovered from barn owl nest boxes in the Midlands (n = 37) and the South East of Southern Great Britain (n = 34). The number of pellets dissected in each region is provided within parentheses under absolute prey numbers. The group 'Other' consists of unidentified prey items and the skulls of birds and frogs recovered from the Midlands.

a)

Barn owl prey items	Absolute prey numbers		Frequency of occurrence (%)		Relative occurrence (%)	
	Midlands (n = 184)	South East (n = 138)	Midlands	South East	Midlands	South East
Field vole (*Microtus agrestis*)	170	117	92.39	84.78	53.79	51.76
Wood mouse (*Apodemus sylvaticus*)	29	53	15.76	38.4	9.17	23.45
Common shrew (*Sorex araneus*)	57	24	30.97	17.39	18.03	10.61
Pygmy shrew (*Sorex minutus*)	21	7	11.41	5.07	6.64	3.09
Bank vole (*Myodes glareolus*)	18	17	9.78	12.31	5.69	7.52
House mouse (*Mus Musculus*)	9	3	4.89	2.17	2.84	1.32
Rat (*Rattus sp.*)	6	1	3.26	0.72	1.89	0.44
Other	6	4	3.26	2.89	1.89	1.76

b)

Barn owl prey items	Absolute prey numbers		Liveweight equivalent (g)		Percent by weight (%)	
	Midlands (n = 184)	South East (n = 138)	Midlands	South East	Midlands	South East
Field vole (*Microtus agrestis*)	170	117	3570	2457	64.81	60.23
Wood mouse (*Apodemus sylvaticus*)	29	53	522	954	9.47	23.38
Common shrew (*Sorex araneus*)	57	24	456	192	8.27	4.71
Pygmy shrew (*Sorex minutus*)	21	7	84	28	1.52	0.68
Bank vole (*Myodes glareolus*)	18	17	288	272	5.22	6.66
House mouse (*Mus Musculus*)	9	3	108	36	1.96	0.88
Rat (*Rattus sp.*)	6	1	360	60	6.53	1.47
Other	6	4	120	80	2.17	1.96

Next, the effects of cereal crop landscape composition on the mean number of barn owl prey items recovered per barn owl nest box were examined. An increase in the total area of cereal crops resulted in a significant decrease in the mean number of prey items per barn owl nest box in the South East (β = -0.005, $CI_{95\%}$ = -0.011, -0.0002; t = -2.12, P = 0.038), and a significant increase in the mean number of prey items per barn owl nest box in the Midlands of Great Britain (β = 1.15, $CI_{95\%}$ = 0.59, 1.6; t = 4.31, P < 0.001; Fig. 5.2). None of the other cereal crop landscape composition

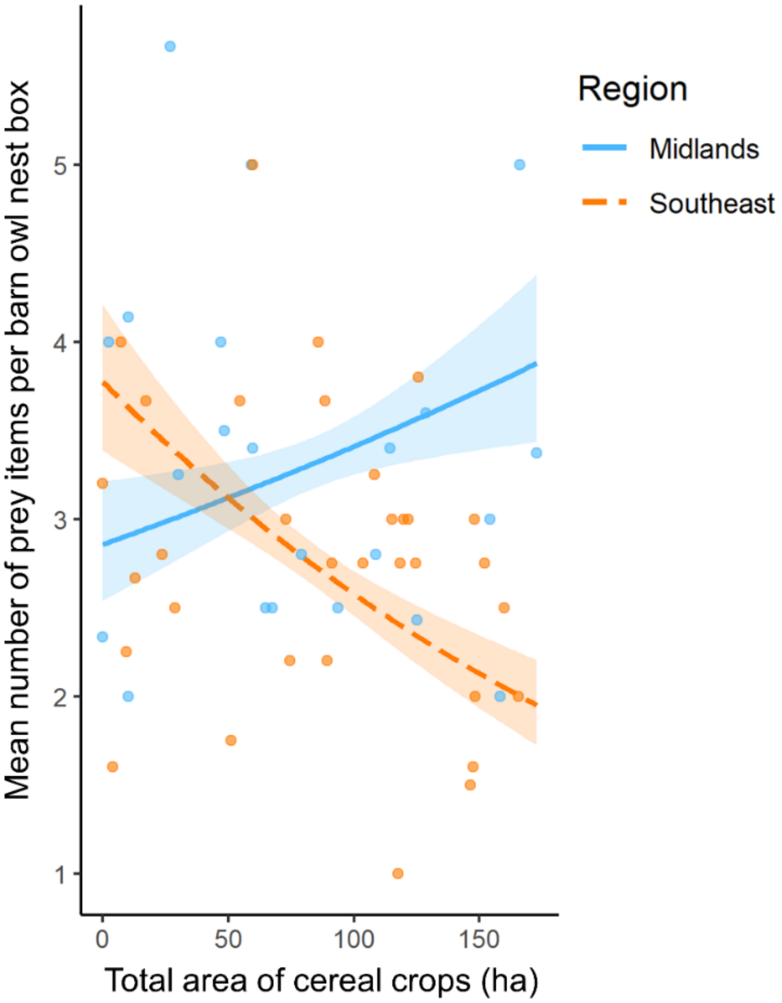

Figure 5. 2. Gaussian distribution GLM of cereal crops showing the relationship between the total area of cereal crops (ha) and the mean number of prey items per barn owl nest box between regions. The shaded areas represent 95% confidence intervals.

metrics, and the interactions of cereal crop landscape composition metrics with region, significantly predicted the mean number of prey items per barn owl nest box (Table 5.4). Similarly, none of the cereal crop landscape composition metrics, and the interactions of cereal crop landscape composition metrics with region, significantly predicted the diversity of prey items per barn owl nest box (Table 5.4).

Table 5. 4. Generalised linear models with gaussian distribution and log link function predicting the mean number of barn owl prey (model 1) and the diversity of barn owl prey (model 2) in relation to the total area, number of patches and the perimeter:area ratio of cereal crop fields, and crop diversity. Region is included as an interaction effect with all landscape composition metrics in both model 1 and model 2. All significant terms are in bold.

Effects of cereal crop landscape composition on the mean number of barn owl prey (Model 1)			
Model	Model coefficients (CI95%)	t-value	P-value
Intercept	1.15 (0.59, 1.6)	4.31	<0.001
Region	-0.57 (-1.636, 0.363)	-1.14	0.258
Total area (ha)	0.001 (-0.002, 0.005)	0.93	0.353
Number of patches	-0.01 (-0.048, 0.016)	-0.9	0.371
Perimeter:area ratio	0.11 (-0.071, 0.3)	1.09	0.279
Crop diversity	-0.28 (-1.196, 0.558)	-0.64	0.523
Total area (ha) × Region	**-0.005 (-0.011, -0.0002)**	**-2.12**	**0.038**
Number of patches × Region	0.02 (-0.031, 0.078)	0.81	0.417
Perimeter:area ratio × Region	-0.06 (-0.365, 0.284)	-0.37	0.706
Crop diversity × Region	1.26 (-0.069, 2.678)	1.77	0.082

Effects of cereal crop landscape composition on barn owl prey diversity (Model 2)			
Model	Model coefficients (CI95%)	t-value	P-value
Intercept	-0.26 (-0.889, 0.227)	-0.96	0.338
Region	-0.61 (-1.594, 0.343)	-1.23	0.225
Total area (ha)	-0.0009 (-0.006, 0.004)	-0.34	0.735
Number of patches	0.02 (-0.019, 0.066)	1.01	0.315
Perimeter:area ratio	-0.12 (-0.351, 0.123)	-1.03	0.305
Crop diversity	-0.86 (-2.153, 0.261)	-1.4	0.169
Total area (ha) × Region	0.0006 (-0.005, 0.007)	0.17	0.859
Number of patches × Region	-0.01 (-0.081, 0.041)	-0.6	0.549
Perimeter:area ratio × Region	0.03 (-0.311, 0.391)	0.17	0.859
Crop diversity × Region	1.34 (-0.237, 3.056)	1.58	0.121

5.5 Discussion

While several studies have examined the diet of the barn owl globally (Bontzorlos, 2005; Tores *et al.*, 2005; Hindmarch and Elliott, 2015; Kross *et al.*, 2016), as well as in the United Kingdom (Glue, 1967; Glue, 1974; Love *et al.*, 2000; Bond *et al.*, 2004; Meek *et al.*, 2012), seldom has any study examined the effects of cereal crop landscape composition on small mammal prey in the diet of the barn owl. In this study, the effects of cereal crop landscape composition (the most dominant crop type in the UK) on small mammal prey of the barn owl is determined. Field voles were the most dominant prey type in both the Midlands and the South East of Great Britain, both in number and live weight equivalent. Next, an increase in the the total area of cereal crops had a negative impact on barn owl prey in the South East of Great Britain, predicting a significantly lower mean number of prey items per barn owl nest box in the South East compared to the Midlands.

The cereal crop landscape composition in the Midlands differed significantly in part to the cereal crop landscape composition in the South East of Great Britain. The total area of cereal crops and crop diversity around barn owl nest boxes in the South East of Great Britain was significantly greater and higher, respectively, compared to the Midlands. These results are contrasting to the findings in Chapter 2, where Midlands had a significantly greater total area and greater perimeter:area ratio of crops in general, compared to the South East of Great Britain. In Chapter 2, the cereal crop landscape composition was determined from a total of 106 nest boxes and 192 nest boxes from the Midlands and the South East, respectively, compared to 37 nest boxes and 34 nest boxes in this study.

Therefore, the smaller sample size of nest boxes in this study may not be representative of the cereal crop landscape composition of the entire Midlands and the South East of Great Britain. Furthermore, the geospatial dataset on agricultural land use used in Chapter 2 was from 2016 to 2018, while the current study uses geospatial dataset from 2019 alone. Therefore, the contrasting findings in cereal crop landscape composition can also be attributed to the temporal difference in the geospatial dataset used for this study.

The dietary composition of the barn owl was found to be similar to several other studies in the United Kingdom (Love *et al.*, 2000; Bond *et al.*, 2004; Meek *et al.*, 2012), with the field vole (*Microtus agrestis*) being the predominant prey species in the diet of the barn owl, both in number and liveweight equivalent, irrespective of region in the United Kingdom. Meek *et al.* (2012) show that barn owls in the UK prey on field voles, simply because of their availability. While the authors suggest that a decrease in the number of field voles does not reflect the field abundance of voles, they suggest that barn owls exploit areas that are more profitable regardless of prey type. The second most predominant prey in the diet of the barn owl differed between regions, with the common shrew (*Sorex araneus*) predominating the diet of the barn owls in the Midlands, and wood mice (*Apodemus sylvatics*) predominating the diet of the barn owls in the South East. Barn owls are shown to be opportunistic predators, easily switching between prey depending on the field abundance of prey species (Tores *et al.*, 2005). Therefore, it is of no surprise that barn owls in the South East preyed more on wood mice compared to the barn owls in the Midlands that preyed more on common shrews, where the occurrence of wood mice and the common shrew can be explained by the differences in the landscape composition of cereal crops. These results can also be consistent with the energetic demands of breeding barn owls; In the Midlands, barn owls compensated for the amount of food consumed as a result of lower consumption of wood mouse (high liveweight equivalence) compared to the South East, by a greater consumption of the common shrew (less liveweight equivalence) compared to the South East of Great Britain. Furthermore, five other prey species were also found in the diet of the barn owl similar to previous studies affirming that barn owls are opportunistic predators and exploit areas that are profitable in catchability (Meek *et al.*, 2012).

When the effects of cereal crop landscape composition on the mean number of prey items per barn owl nest box were examined, an increase in the total area of cereal crops had a negative impact on barn owl prey in the South East of Great Britain, predicting a significantly lower mean number of prey items per barn owl nest box in the South East compared to the Midlands. The homogenisation of habitats because of agriculture results in the loss of diverse natural habitats that are required for the sustenance of small mammal communities (Michel *et al.*, 2007). Furthermore, cereal crops are less than optimal habitats for small mammals such as voles (Heroldová *et al.*, 2007; Rodríguez-Pastor *et al.*, 2016). For example, traditionally-tilled cereal crop fields provided poor refuge and shelter for common voles, compared to agricultural landscapes with greater structural heterogeneity (e.g. plots with longer field margins; Santamaría *et al.*, 2019). Given that cereal crop cultivation in the South East was significantly greater than the Midlands of Great

Britain, it is of no surprise that significantly lower mean number of small mammal prey items were recovered from barn owl nest boxes in the South East compared to the Midlands.

Linear features such as hedgerows in agricultural fields were rapidly lost since the advent of agricultural intensification in the UK, with removal of around 50% of hedgerow stock (Rackham, 1997; Robinson and Sutherland, 2002). However, at present, reforms such as improvements in the Common Agricultural Policy have enabled enhanced hedgerow management strategies and retention of grass margins to aid in farmland biodiversity conservation (Gelling, Macdonald and Mathews, 2007). Hedgerows and grass margins can constitute the sole habitat for certain small mammal species in a heavily fragmented agricultural landscape (Michel, Burel and Butet, 2006; Shore *et al*., 2005). For example, Gelling, Macdonald and Mathews (2007) showed that the total amount of hedgerows in agricultural landscapes resulted in an increase in small mammal biomass. Similarly, bank voles, wood mouse and common shrews are shown to be the most abundant species in grass margins compared to conventional field edges (Shore *et al*., 2005). Therefore, by increasing and protecting linear features such as hedgerows and grass margins in agro-ecosystems, small mammal numbers can be maintained.

Finally, the cereal crop landscape composition around barn owl nest boxes had no significant impact on the diversity of barn owl prey recovered from individual barn owl nest boxes in the Midlands and the South East of Great Britain. Barn owls are opportunistic predators, switching prey species depending on the field abundance of prey and foraging in profitable areas (Tores *et al*., 2005). A study by Arlettaz *et al*. (2010) showed that barn owls forage in areas that more accessible and with higher prey abundance over areas with higher prey density. Furthermore, other prey species such as yellow-necked mouse and harvest mouse were absent in this study, either because of observer error in identification or because of low sampling effort. Therefore, it is likely that the diversity of small mammal prey represented in the diet of the barn owl is not representative of the diversity of prey in cereal crop landscapes. As a result, the cereal crop landscape composition did not significantly predict the diversity of small mammal prey recovered from barn owl nest boxes.

Overall, the findings of this study shows that the constituent prey species of the barn owl diet are primarily composed of small mammals, while the composition of the small mammal prey might differ as shown by other studies (Love *et al*., 2000; Balestrieri *et al*., 2019). Furthermore, increasing the habitat complexity of cereal crop fields in Great Britain can benefit barn owls by increasing the catch of small mammal prey during the breeding season thereby influencing the probability of a successful breeding attempt. Similarly, agricultural landscapes in Great Britain must be coupled with small islands of natural habitats along with enhanced management of hedgerows to ensure the protection of all farmland species alike, including farmland raptors such as the barn owl. Future studies on the foraging behaviour of barn owl in agricultural landscapes can provide more information on the impact of the agricultural landscape composition of the most dominant crop type – cereal crops, on the diet of a conservation flagship species such as the barn owl in Great Britain. The implications of which, can be used to comprehensively understand the role of the contribution of food resources in barn owl reproductive potential.

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Chapter 6

Study Limitations, Conclusions and Recommendations

6.1 Study limitations

Barn owl breeding data archived by the British Trust for Ornithology (BTO) was extensively used in producing this thesis to understand the effects of the agricultural landscape composition on aspects of barn owl reproduction. Altogether, a total of 1489 breeding attempts from 740 unique barn owl nest boxes between 2012 and 2018 were used in this thesis. Using secondary data such as the breeding records of barn owls populated by licensed bird ringers comes with its challenges (Anderson and Green, 2009). For example, a total of 11,000 breeding records were acquired from the BTO at the initial stage of this study. While the 11,000 breeding records provided information on the number of barn owl individuals ringed between 2012 and 2018, the incompleteness of the information on the breeding data of barn owls must be addressed. For example, the brood size and the corresponding body mass of barn owl nestlings were only available for 13% (the total sample size in this thesis) of the 11,000 breeding records. Furthermore, information on the outcome of each breeding attempt (number fledged) was not available for nearly 95% of the breeding records and could not be included in any of the studies presented in this thesis. Despite the relatively small sample size in breeding records (n = 1489) compared to the original dataset (n = 11,000), biologically significant results were obtained in relation to the effects of the agricultural landscape composition on aspects of barn owl breeding such as the brood size, mean body mass of barn owl nestlings, maternal body condition, and diet.

Among the dependent variables used in this thesis, human error in the measurement of the body mass of barn owl nestlings, the measurement of wing chord lengths and the body mass measurement of female adult barn owls were considered, but the lack of information on the method or equipment used in the measurements made it impossible to account for discrepancies. From personal observation, on-field measurements of nestling and adult barn owl body mass are collected from different weighing equipment with different calibrations. For example, nestling body mass can be weighed using either a weighing scale or a spring balance of different makes, while adult barn owls are weighed using a spring balance (Pers. obs.). Therefore, it was not possible to account for the differences in body mass that could have risen as a result of using different weighing equipment. However, the wing chord lengths used in Chapter 3, can be a consistent measure between individuals as this is a linear measurement independent of equipment calibration. Whether the wing chord measurements were taken more than once to complement the accuracy of the measures could not be confirmed. Even with the shortcomings of human error in measurement, a general trend in the negative impacts of the landscape composition of cereal crops on maternal barn owl body condition and brood sizes was observed.

Due to the Schedule 1 protected status of the barn owl under the Wildlife & Countryside Act 1981, the exact location of the barn owl nests was not provided, but an approximate location within a 10km^2 area was given. Consequently, the agricultural landscape structure that was extracted around the nest boxes of breeding barn owls might not truly reflect the agricultural landscape composition around the precise location of barn owl nest boxes. However, since this was the case with all nest records originating from the Midlands, the South East and the South West of Great Britain, the relative effects of the extraction of landscape composition metrics from imprecise nest box locations between regions can be counteracted.

The geospatial dataset used in this study corresponded with the year of barn owl breeding in Chapter 2, Chapter 3, and Chapter 5, however, the geospatial dataset on pesticide use in Chapter 4 provided information on the average use of pesticides between 2012 and 2016. Consequently, the breeding records from each individual year between 2012 and 2016 from unique nest boxes were used to predict the impact of the dominant fungicides (chlorothalonil and diflufenican) and herbicides (glyphosate and flufenacet) used in the cultivation of cereals on barn owl brood size and nestling body condition. Chapter 3 shows that the use of flufenacet has a negative impact on the brood size of barn owls but not on nestling body condition. Nevertheless, the effects of flufenacet and the other candidate herbicides (glyphosate) and fungicides (chlorothalonil and diflufenican) could be more pronounced in affecting barn owl brood sizes provided the geospatial information on pesticide application was available on a yearly basis, but this remains to be confirmed.

Finally, barn owl pellets were provided by volunteer bird-ringers from across southern Great Britain. While the sample sizes of the nest box that the pellets originated from were deemed sufficient for the Midlands (n = 37) and the South East (37), a lack of pellets originating from six nest boxes in the South West made it non-viable for the pellet samples to be included in Chapter 5. Furthermore, despite the number of pellet dissections proving sufficient in the recovery of small mammal prey in the diet of the barn owl from the Midlands and the South East, the results on the landscape composition of cereal crops in the Midlands and the South East contrasted the results on the landscape structure of cereal crops in Chapter 2. In Chapter 5, it was shown that South East had a greater total area of cereal crops and higher crop diversity compared to the Midlands. However, the landscape composition of cereal crops in Chapter 5 were only assessed around 37 nest boxes in the Midlands and 34 nest boxes in the South East compared to 106 nest boxes in the Midlands and 302 nest boxes in the South East in Chapter 2. Regardless of these differences in the landscape composition of cereal crops between regions, a significant negative impact was observed in the number of prey items recovered in the diet of the barn owl in relation to the total area of cereal crops, complementing the results of Chapter 2, where a greater total area of cereal crops predicted smaller brood sizes.

Bird ringing in the United Kingdom has become an important research tool in the field of ornithology over the past 100 years and has provided information on home ranges, dispersal capabilities, survival, and body condition of ringed birds (Anderson and Green, 2009). While Evans *et al.* (1999) have suggested that collecting biometrics such as body size and mass can help interpret the future changes in bird populations, seldom are these practices carried out by all ringing volunteers. For example, the completeness of the original barn owl dataset with 11,000 records can be used for determining dispersal capabilities, home ranges and survival of barn owls in Great Britain, but the lack of data on barn owl brood size and corresponding body mass of nestlings rendered most of the breeding records from the original dataset non-viable for determining barn owl reproductive potential across a wider region. Furthermore, bird-ringing initiatives in the United Kingdom are either predominantly self-financed or supported by smaller non-governmental organisations. As a result, the financial constraints in bird-ringing activity, and the scope of data collection can be limited. Furthermore, it is possible that bird-ringing volunteers have reservations about handling nesting adult barn owls to minimise stress and disturbance. Therefore, it is imperative to involve bird-ringing volunteers through the stages of research planning and execution, such that the targeted contribution of data can contribute to the greater good of bird conservation.

6.2 Conclusions

The aim of this thesis was to determine the impact of agricultural landscape structure and pesticide use on barn owl brood size and body mass of nestlings, and maternal barn owl body condition and diet of barn owls in Great Britain. Previous studies on barn owl reproduction have suggested that barn owl breeding in relation to habitat type is similar to that expected by chance (Meek *et al.*, 2009; Frey *et al.*, 2011). Furthermore, Frey *et al*. (2011) suggested that barn owls will always find suitable foraging areas to aid in their survival. However, the limitations of these studies included limited coverage of study area and were based on the assumption that the geospatial data on land use remained constant between the years the land use was mapped and the period of barn owl breeding data that was used (Meek *et* *al*., 2009; Frey *et al*., 2011). Unlike previous studies, this thesis focuses on the multiscale effects of barn owl breeding across the three regions of Great Britain namely the Midlands, the South East and the South West. Furthermore, this thesis uses the recently introduced geospatial data on crop cover that corresponds to the period of the collected barn owl breeding data, to determine barn owl reproductive potential.

The results from Chapter 2 shows that among all crop types, fruit/forage crops had a significant positive impact on barn owl brood size, irrespective of region. Fruit/forage crops are intensively managed agricultural habitats, forming less than optimal habitats for small mammal prey of barn owls. However, fruit/forage crops can have adjoining linear features such as hedgerows and grass margins which can support small mammal prey populations, thereby offering greater food resources for breeding barn owls resulting in large barn owl brood sizes (Shore *et al*., 2005; Gelling, Macdonald and Mathews, 2007). On a regional level, a greater total area of cereal crops predicted smaller brood sizes, while a greater number of cereal crop patches predicted larger brood sizes in the Midlands, compared to the South East, but not the South West of Great Britain. A commercially large area of cultivated cereal crops can result in the homogenisation of the habitat with a lesser number of linear features such as hedgerows that are vital for small mammals in sustenance in agricultural landscapes (Gelling, Macdonald and Mathews, 2007). An increase in the number of patches of cereal crop fields results in a heterogeneous landscape with a mixture of linear features such as hedgerows, and different crops that provide a suitable habitat for small mammal populations to persist in numbers in the Midlands (Michel, Burel and Butet, 2006; Gelling, Macdonald and Mathews, 2007). These results are congruent with the findings in agricultural land use where the Midlands despite having a larger total area of cereal crops, also had a greater number of patches and crop diversity compared to the South East or the South West of Southern Great Britain (see Chapter 2). In contrast, the mean body mass of barn owl nestlings increased with a total area of cereal crops but decreased with a greater number of cereal crop patches in the Midlands, compared to the South East, but not the South West of Great Britain. Among barn owls, it is shown that when an extra parental effort is necessary to provide for larger broods, a reduction in brood size occurs (Roulin, Ducrest and Dijkstra, 1999). Therefore, a greater mean body mass of barn owls in relation to a greater total area of cereal crops can be a result of a reduction in brood sizes where the amount of food delivered to barn owl nestlings is shared between nestlings of smaller brood sizes. Similarly, an abundance of food resources that can be associated with a greater number of cereal crop patches can result in a lower mean body mass of barn owl nestlings where the amount of food delivered to barn owl nestlings is shared between nestlings of larger brood sizes. Despite the overall negative effects of cereal crops on barn owl brood sizes and consequently on the mean body mass of barn owl nestlings, simulations of cereal crop generalised linear mixed models showed that agricultural landscape structure alone is a poor predictor of barn owl brood size. The results from this chapter show that barn owl breeding can be affected by knock-on effects of agriculture and agricultural land use on aspects responsible for barn owl reproduction such as maternal body condition and availability of food resources which were further investigated in this thesis.

The barn owl reproductive potential is dependent on the availability of food resources around the nesting sites. For example, the parental effort in the barn owl is asymmetric, where the male barn owls deliver food to the nesting female barn owls (Durant, Massemin and Handrich, 2004). Furthermore, it is shown that the female barn owls adjust their clutch size depending on the capability of the male barn owl in delivering food (Durant, Gendner and Handrick, 2004). However, barn owls trade-off between the investment of effort in the production of offspring with their own survival in unlikely scenarios (Durant, Gendner and Handrick, 2004). The results of Chapter 2 showed a general negative trend of cereal crops on barn owl brood size. Although cereal crops were not accurate predictors of barn owl brood size, the effects of the landscape structure of cereal crops on maternal barn owl body condition were investigated. Unlike the results of Chapter 2, where the perimeter:area ratio (habitat complexity) had no significant effect on barn owl brood size, Chapter 3 showed that an increase in the perimeter:area ratio of cereal crops had a significant positive effect on maternal barn owl body condition resulting in larger barn owl brood sizes. An increase in the habitat complexity of cereal crop fields can be attributed to a greater number of linear features such as hedgerows that can sustain small mammal prey in agricultural landscapes consequently resulting in larger barn owl brood sizes. Furthermore, the simulations of the generalised linear mixed model of the landscape structure of cereal crop fields showed that the habitat complexity of cereal crop fields along with the body condition of maternal barn owls was more accurate in predicting barn owl brood sizes compared to the landscape composition of cereal crops alone.

Intensive commercial agriculture such as the cultivation of cereal crops in the United Kingdom is associated with the use of chemical agents such as pesticides to increase crop productivity, while impacting farmland biodiversity (Skinner *et al.*, 1997). Present-day pesticides are used on the premise of having non-threatening effects on farmland species under an agreed acceptable risk of toxicity (Finizio and Villa, 2002), however, not much is known about the knock-on effects on apex predators such as the barn owl. In chapter 4, the impact of four commonly used pesticides (by weight) namely herbicides (glyphosate and flufenacet) and fungicides (chlorothalonil and diflufenican) in the cultivation of cereal crops on barn owl brood size and body mass of nestlings was established. Despite flufenacet being the second lowest in the quantity used after diflufenican in the cultivation of cereal crops, flufenacet had a negative impact on barn owl brood size, irrespective of region. Flufenacet is shown to have the highest toxicity in terms of median lethal dosage (LD_{50}), which is the amount of the pesticide that is required to kill half the members of a test population after a specified test duration (lower the LD_{50} values higher is the toxicity to the target organism). Flufenacet had an LD_{50} of 1608mg/kg in birds, compared to glyphosate (LD_{50} = >2000mg/kg), chlorothalonil (LD_{50} = >2000mg/kg), and diflufenican (LD_{50} = >2150mg/kg; Lewis *et al.*, 2016). Furthermore, flufenacet is reported to have high chronic sublethal toxicity to birds (Cech *et al.*, 2022). Consequently, it is likely that bioaccumulation of flufenacet residuals through consumption of small mammal prey can affect the reproductive potential of barn owls resulting in smaller brood sizes, however, the mechanism involved remains to be studied. As a result, the acceptable risks of pesticides established by the pesticide legislation must be revised making use of scientific studies that examine the effects of approved pesticides on non-target organisms.

Finally, the diet of the barn owl in relation to the landscape composition of cereal crops was determined in Chapter 5. In contrast to Chapter 2, where the total area of cereal crops and crop diversity was found to be the highest in the Midlands, the study area in this Chapter showed the opposite where the total area of cereal crops and crop diversity was the highest in the South East compared to the Midlands of southern Great Britain. Congruently, an increase in the total area of cereal crops predicted lower number of prey items in the diet of the barn owl from the South East compared to the Midlands, respectively. Irrespective of the differences in the extent of cereal crop cultivation across Great Britain, the results of this chapter complement the findings of Chapter 2, where an increase in the total area of cereal crops predicted lower barn owl brood sizes. The results of this study showed that barn owls are opportunistic predators such that barn owls in the South East consumed more wood mouse (less liveweight equivalent) to make up for the lack of field voles (high liveweight equivalent), which were consumed more in the Midlands. What remains to be studied is whether the pesticide flufenacet has any impact on small mammal numbers recovered in the diet of the barn owl. It is likely that flufenacet has a negative impact on the number of small mammal prey caught by barn owls, however with the lack of pesticide data covering the period of pellet collection in 2019, it remains to be investigated.

Overall, this thesis demonstrates the intricate network between habitat structure, availability of food resources, and life-history traits such as body condition that can influence the breeding potential of the barn owl in agricultural landscapes. This thesis further highlights the problem in avian ecological studies where there is a need to consider a range of environmental stressors which can influence life-history traits such as the body condition of birds in order to untangle the habitat-dependent effects on reproductive performance. Finally, this thesis shows the need for a scale-dependent approach to understanding the aspects of organismal biology, where the effects, either positive or negative are generated by the immediate environment associated with energetic demands such as investment effort to produce offspring and self-survival.

6.3 Summary of recommendations

This thesis presents empirical evidence on the negative impacts of agriculture, particularly of cereal crops on a conservation flagship species such as the barn owl. Furthermore, it is likely that the agricultural efforts in the United Kingdom are only going to be intensified in the future to meet the needs of an ever-growing human population. Therefore, it is imperative the current state of agricultural landscapes in Great Britain be made more eco-friendly for the sustenance of all farmland biodiversity. The list of recommendations based on the results from Chapter 2 to Chapter 5 in this thesis is provided below:

1) In commercially intensive farms where cereal crop cultivation results in the loss of natural habitats, it is vital to have small islands of natural habitat in-between cultivated crops. A study by Knapp and Řezáč (2015)

has shown that small non-crop habitats can boost arthropod assemblages. An increase in arthropod assemblages can boost the presence of insectivorous small mammals such as shrews, which were found to be the second most dominant prey item in the diet of the barn owl in the Midlands.

2) Similar to the first recommendation, maintaining grass margins in and natural habitats along field edges, can generate the growth of linear features such as the hedgerows and trees that can not only provide perches for foraging raptors (Mirski and Väli, 2021) but can also serve as a refuge to small mammal prey populations (Michel, Burel and Butet, 2006; Gelling, Macdonald and Mathews, 2007).
3) Continued monitoring of the regular use of pesticides can help in making reformed legislative decisions on what is defined as an acceptable risk for the future use of toxic pesticides. For example, the use approval of flufenacet use is set to expire 2024 in the UK (Lewis *et al.*, 2016) and lawmakers must therefore assess the cost-benefit ratio of the future approval of the use of flufenacet to find alternative herbicides.
4) Finally, it is imperative to spread awareness among volunteer bird ringers on the advantages of collecting biometric data such as wing chord lengths and body mass measurements of nestlings, that can be used to assess the body condition and reproductive potential of farmland birds contributing to the greater good of avian conservation through monitoring population changes.

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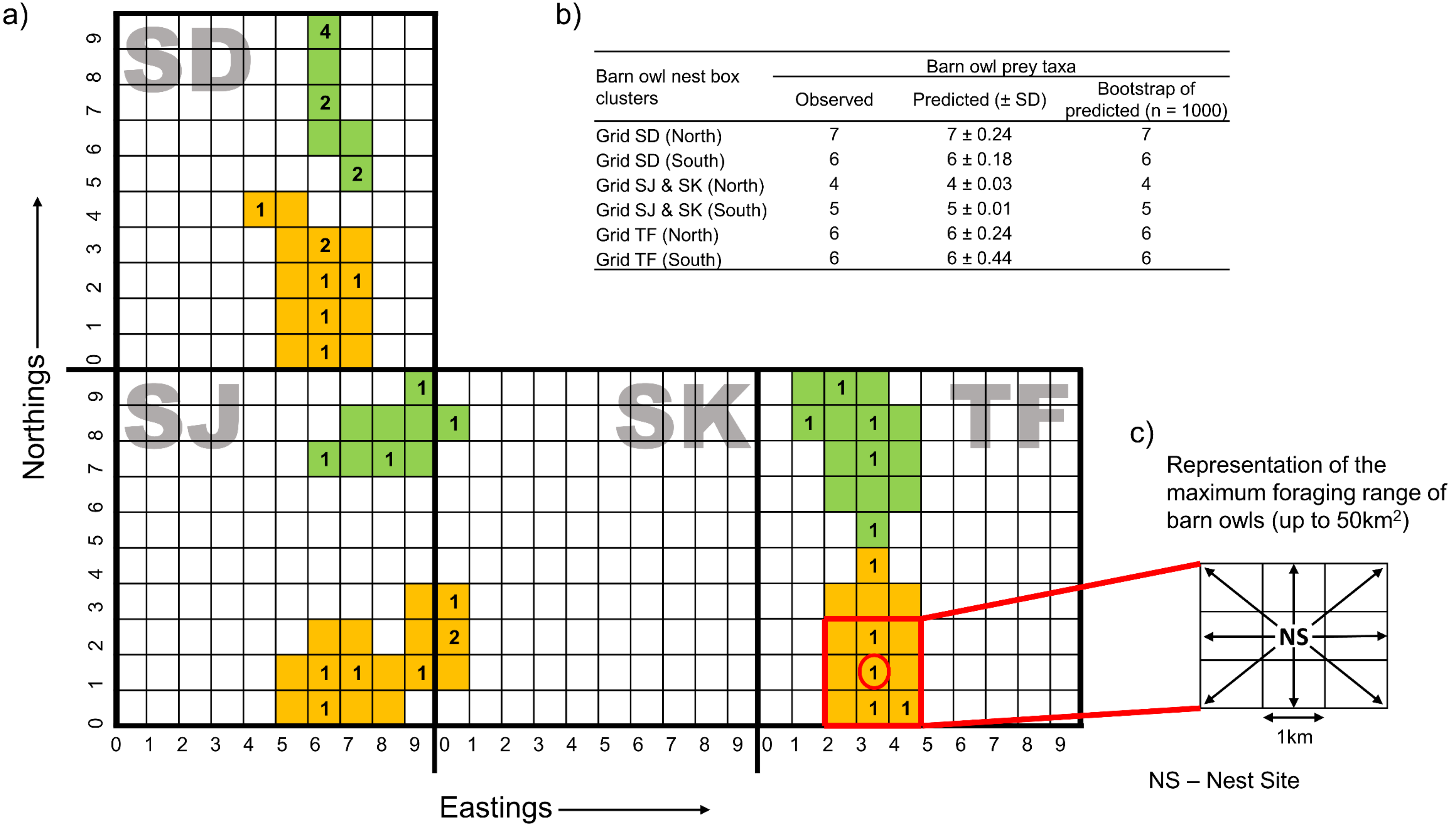
Appendices

Appendix A. *(a) Pellets collected from barn owl nest boxes from grids SD, SJ, SK and TF from the Midlands, and TL, TM and TQ from the South East of Great Britain. The area of each British National Grid corresponds to 1km^2 and the numbers within each grid represent the number of barn owl nest boxes. Nest box clusters were separated by North (green-filled grids) and South (yellow-filled grids), within an area of 50km^2 (Shawyer, 1998) by using the most distant location of a nest box(s) as the point of origin. Overlapping foraging ranges were also filled with the respective colours depending on whether the cluster was situated in the North or South of each grid. (b) Chao 2 nonparametric estimates of all prey items recovered in the diet of the barn owl. Observed values represent the total number of prey species recovered from barn owl nest boxes in each nest box cluster. Predicted values represent the total number of prey species that would be recovered from barn owl nest boxes given the total number of pellet dissections that have been carried out in each nest box cluster. Bootstrap values of the predicted are also provided. (c) Represents the maximum foraging range of barn owls (up to 50km^2) around each nest box in a cluster, in this case the representative nest box is circled in red and the maximum foraging range is demarcated with red lines (in grid TF only).*

a)



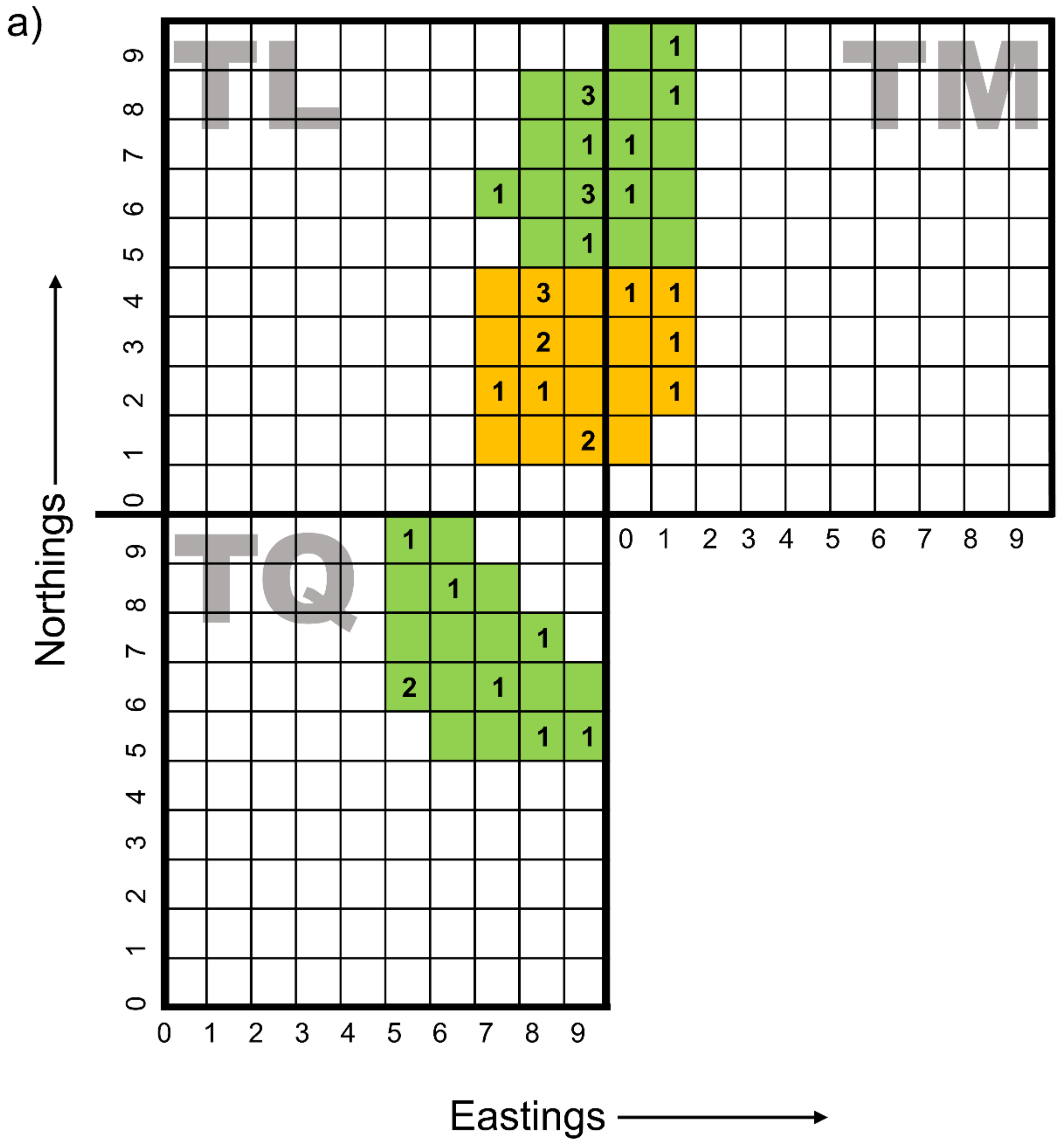
b)

Barn owl nest box clusters	Barn owl prey taxa		
	Observed	Predicted (± SD)	Bootstrap of predicted (n = 1000)
Grid SD (North)	7	7 ± 0.24	7
Grid SD (South)	6	6 ± 0.18	6
Grid SJ & SK (North)	4	4 ± 0.03	4
Grid SJ & SK (South)	5	5 ± 0.01	5
Grid TF (North)	6	6 ± 0.24	6
Grid TF (South)	6	6 ± 0.44	6

c)

Representation of the maximum foraging range of barn owls (up to 50km^2)

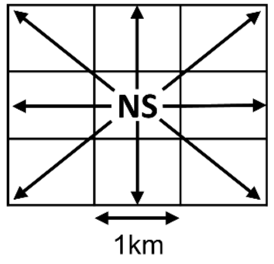
NS – Nest Site



b)

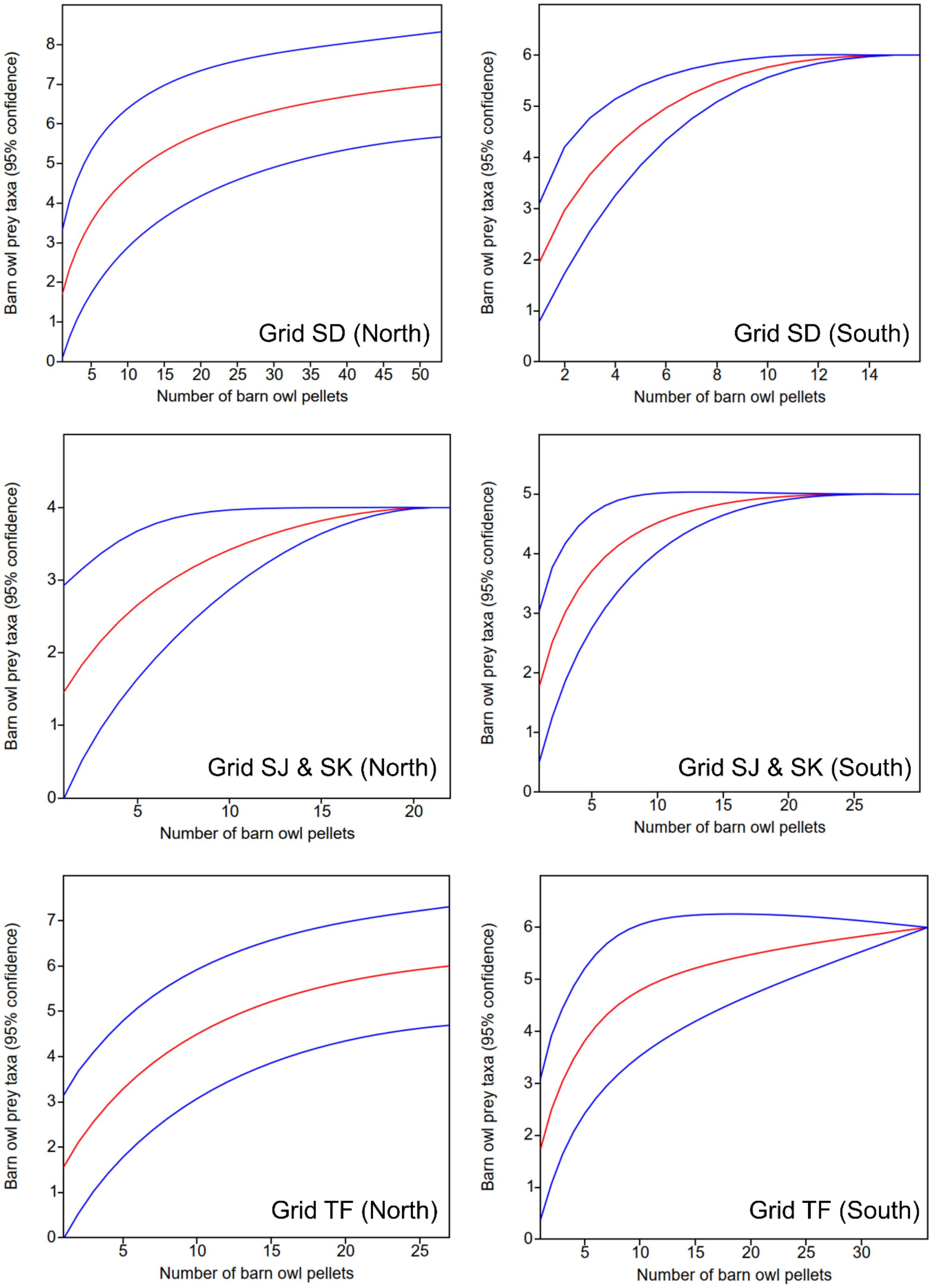
Barn owl nest box clusters	Barn owl prey taxa Observed	 Predicted (± SD)	 Bootstrap of predicted (n = 1000)
Grid TL & TM (North)	6	6 ± 0.44	6
Grid TL & TM (South)	7	7 ± 1.27	8
Grid TQ (North)	6	6 ± 0.16	6

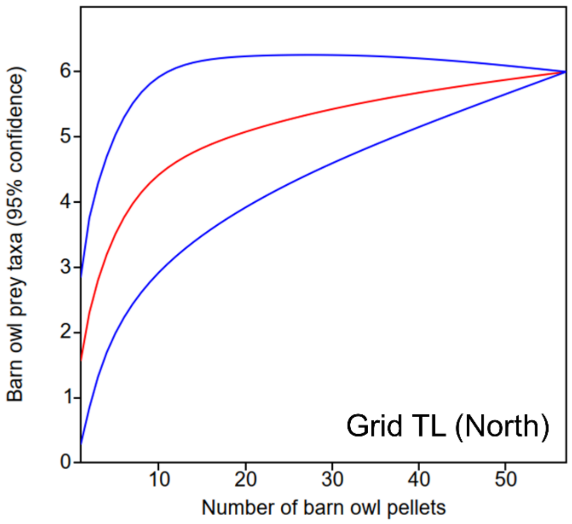
c) Representation of the maximum foraging range of barn owls (up to 50km^2)

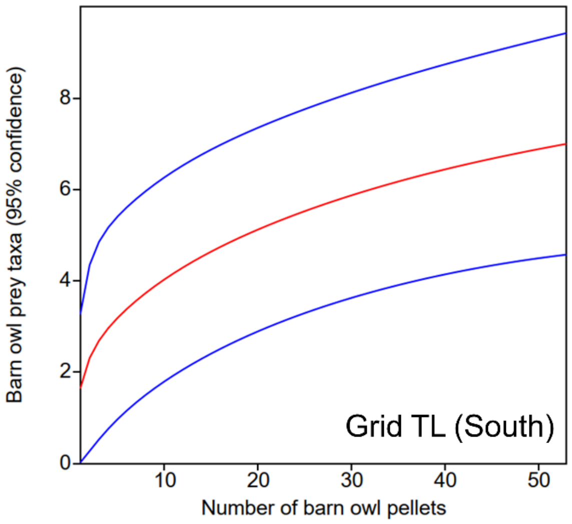


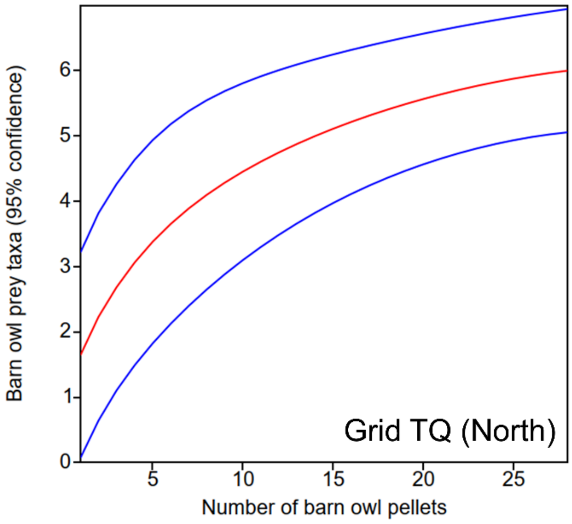
NS – Nest Site

Appendix B. *Species accumulation curves for each nest box cluster from the Midlands and the South East of Great Britain. The red line represents the relationship between the number of barn owl pellets dissected and the number of barn owl prey taxa recovered. The blue lines represent 95% confidence intervals.*




Grid TL (North)
Barn owl prey taxa (95% confidence)
Number of barn owl pellets
0
1
2
3
4
5
6
10
20
30
40
50


Grid TL (South)
Barn owl prey taxa (95% confidence)
Number of barn owl pellets
0
2
4
6
8
10
20
30
40
50


Grid TQ (North)
Barn owl prey taxa (95% confidence)
Number of barn owl pellets
0
1
2
3
4
5
6
5
10
15
20
25

Appendix C. *Shapiro-Wilk's test for normality and Levene's test for homogeneity of variance between groups of the dependent variables used in generalised linear models 1 and 2. Number of barn owl nest boxes are provided within parentheses (Chapter 5).*

Dependent variables	Test for normality of distribution		Test for homogeneity of variance between groups
	Shaprio-Wilk's test for normality		Levene's test for homogeneity of variance based on medians
	Midlands (n = 37)	South East (n = 34)	
Mean number of prey items per barn owl nest box	W = 0.97, P = 0.488	W = 0.97, P = 0.745	$F_{1,69}$ = 1.33, P = 0.252
Diversity of prey per barn owl nest box	W = 0.95, P = 0.181	W = 0.94, P = 0.07	$F_{1,69}$ = 2.57, P = 0.113