Improving sustainability and monitoring within the UK pheasant release system

Submitted by Andrew David William Hall to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Psychology in December 2019.

Signature:

Abstract

Between 39-57 million pheasants (*Phasianus* colchicus) are reared and released into the UK each year to accommodate recreational shooting. When carried out well, the associated land management can be very positive for the environment. However, releases at high densities can cause significant detrimental impacts for the wildlife around release sites. To improve the environmental sustainability of the shooting industry, methods must be found to; reduce the numbers of birds released without adversely affecting the shooting industry, increase knowledge and understanding of the impacts of pheasant releases on wildlife, and ensure that methods of monitoring pheasant populations are robust and reliable.

I showed that two separate rearing enhancements can be combined within a commercial rearing system and lead to greater pheasant harvests while still releasing the same numbers, so future release sizes can be reduced while harvest rates are maintained. This was achieved by the provisioning of perching material and providing an improved diet during rearing that resulted in improved pheasant survival post-release, enabling more to contribute to the harvest. Enhanced pheasants were harvested at rates 16-17% higher than Control pheasants on shoots releasing <601 or >2000 pheasants but 6% lower on shoots releasing 601-2000 pheasants. When release date was considered and not release size, shoots that released prior to August 22nd shot proportionately more Enhanced birds while shoots that released after shot proportionally more Control. Enhanced Rearing was cost-effective, only increasing the average cost per pheasant by 2.6%. Enhanced pheasants also flew higher, had larger hearts, larger breast muscles, thicker tarsi, gained weight more

slowly over time, and impact invertebrates and habitats in and around the release pen no more than traditionally reared pheasants. Higher flying pheasants were shot at higher rates early in the shooting season but lower rates by the end. The overall flight performance of the pheasant population as a whole does not change over the course of the shooting season.

Releasing pheasants can lower total invertebrate biomass, slug counts, and detritivore counts within the release pen by 4 weeks post-release when overall invertebrate abundance is high, but this effect is removed by 9 weeks post-release. Conversely, when overall invertebrate abundance is low, there is little effect of releasing pheasants on invertebrates within release pens 4 weeks post-release, but by 9 weeks post-release, pen interiors can have higher total invertebrate biomass, total invertebrate counts, slug counts, and beetle counts. Releasing pheasants at higher stocking densities in one year can, prior to releases in following years, reduce the invertebrate biomass within the release pen, reduced detritivore counts both inside and outside of the pen, and increase slug counts both inside and outside of the pen.

I created a correction factor that accounts for the deterioration rate of the Multi-Tag patagial wing tag which is widely used for marking gamebirds. This allows past and future datasets using this tag to increase the accuracy of their findings. Even with the correction factor, I recommend that Multi-Tags not be used for long-term (>1 year) studies. I improved the accuracy of aging pheasants using proximal primary feather features by 1.3% by adding feather mass as an additional variable to

length and diameter. I also found that machine learning may be overall less effective at aging pheasants via the proximal primary method alone. Finally, I discussed the implications of my findings and how they could impact wildlife conservation, pheasant and shoot management, and monitoring gamebird populations. I also identified several areas for potential future study.

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Acknowledgements

This PhD has taken over 4 years to complete and would not have been possible without the support of many other people. Below are a few of those that most impacted my research in no particular order.

My father, for helping me build pheasant perches, find practical ways of actually carrying out my research ideas, and doing just about anything that I needed a hand with.

Dr Joah Madden, who has guided me along the very long road to finally submitting this PhD.

The Game and Wildlife Conservation Trust, who not only part funded this PhD but also provided as much assistance as they were able to impart whenever I needed it.

Dr Rufus Sage, my secondary supervisor who has provided me with invaluable knowledge on all things pheasant related.

Dr Maureen Woodburn, who has provided me with as much information regarding pheasant tagging as my heart could wish for.

Austin Weldon, who runs the Loddington shoot and was unimaginably accommodating to me as I ran around getting in the way on his shoot days. He also provided me with a roof over my head both in a mobile home whose plumbing required constant attention and at his own home when said plumbing inevitably failed. Thank you for the hot showers.

Matt Coup, game keeper at Loddington and helpful in any practical matter we could think of.

The Brown Family at Sutton Court Game Farm, for listening to my insane ideas about rearing pheasants a little differently and letting me impose myself on their very strict and work-intensive pheasant rearing system.

Mark Whiteside, whose research formed the basis of the Enhanced Rearing methodology and who has been incredibly helpful whenever I needed someone capable of imparting complex issues in a manner my often slow-acting brain was capable of digesting.

Michael Weiss, whose ability to make my cave-man brain understand statistics was all that kept me from putting my fist through my laptop on multiple occasions.

My Fiancé, Ruby, for everything she has done to keep my sanity, such as dealing with my cabin-fevered ramblings for the past 12 months while I’ve been stuck at home all day writing up this thesis.

Finally, all the shoots that allowed me to carry out research in some way upon their ground, be that counting the tagged pheasants in the game bags or letting me wander about their release pens digging pitfall transects for invertebrates.

This PhD was jointly funded by the University of Exeter and the Game and Wildlife Conservation Trust.

Declaration

This thesis contains five data chapters. Each was written as a manuscript for publication. However, due to the inter-connected themes of the work, some chapters contain references to results shown in previous chapters. Additionally, some information may also be redundant or repeated.

While the candidate made substantial contributions to the manuscripts and is fully responsible for the work presented in this thesis, where the first person is used throughout the thesis it is used in the plural (‘we’) to reflect contributions from co-authors. This is also the case in the introductory Chapter (Chapter 1) and general discussion (Chapter 7) for consistency. Contributions by co-authors are detailed for each manuscript below. Dr Joah Madden and Dr Rufus Sage were involved in designing the project, guided data collection, and provided comments on drafts of chapters. All data used in this thesis was collected during the period of the PhD, with the exception of preliminary findings from the GWCT’s National Game Marking Scheme, which was used as a real-world example for the application of the correction factor developed in Chapter 5. The data was kindly provided by Dr Maureen Woodburn (GWCT).

Chapter 2: **Can adding dietary and pen enrichment improvements to a commercial pheasant rearing environment lead to increased pheasant harvest?**

Hall ADW., Madden JR., Sage R.

The candidate designed the project methodology under the guidance of Dr Joah Madden and Dr Rufus Sage, collected the data, analysed the data, and wrote the manuscript. All authors provided feedback on the drafts of the paper.

Chapter 3: **Does Enhanced Rearing alter the flight performance of pheasants and does the flight performance of a pheasant impact the likelihood of being shot?**

Hall ADW., Madden JR., Sage R.

The candidate designed the project methodology under the guidance of Dr Joah Madden and Dr Rufus Sage, collected the data, analysed the data, and wrote the manuscript. All authors provided feedback on the drafts of the paper.

Chapter 4: **The impact of pheasants on the invertebrates and habitats within the release pen?**

Hall ADW., Madden JR., Sage R.

The candidate designed the project methodology under the guidance of Dr Joah Madden and Dr Rufus Sage, collected the data, analysed the data, and wrote the manuscript. All authors provided feedback on the drafts of the paper.

Chapter 5: **How accurate is monitoring pheasant populations via differing patagial wing tags?**

Hall ADW., Madden JR., Sage R, Woodburn, MIA.

The candidate designed the project methodology under the guidance of Dr Joah Madden and Dr Rufus Sage, collected the data, analysed the data, and wrote the manuscript. Additionally, Dr Maureen Woodburn (GWCT) provided preliminary data from the NGMS. All authors except Dr Woodburn provided feedback on the drafts of the paper.

Chapter 6: **Can aging pheasants via the Proximal Primary Method be improved?**

Hall ADW., Madden JR.

The candidate designed the project methodology under the guidance of Dr Joah Madden, collected the data, analysed the data, and wrote the manuscript. All authors provided feedback on the drafts of the paper.

Chapter 1 – The pheasant shooting industry, its impacts on UK wildlife, current methods of improving and measuring sustainability within it, and how my research will aim to improve these methods

1.1 The current state of shooting and pheasant releases in the UK

1.1.1 The Shooting industry and the mass release of pheasants

In the UK today, few non-native species are intentionally released into the wild due to potential adverse impacts to native wildlife such as over-competition, alteration of natural environments, and the spread of disease (Manchester and Bullock, 2000; Sakai *et al.*, 2001). However, this is not the case for the tens of millions of common pheasants (*Phasianus colchicus*) released each year to supplement wild populations for shooting. There has been a dramatic increase in the number of pheasants released over the past five decades, with average release numbers on the land where shooting takes place (shot land) between 1962 and 1985 increasing from 60 to 260 peasants per km^2 (Hill and Robertson, 1988b), an overall 9-fold increase in release numbers between 1961-2011 according the National Gamebag Census Index (Parrott, 2015), an average of 4.3% increase in release numbers each year between 1960-2014 (Robertson *et al.*, 2017), and current yearly pheasant release figures at 39-57 million (Aebischer, 2019). This directly adds an estimated additional 41,000 tonnes of biomass into the UK countryside, 16 times higher than any other wild bird species (Parrott, 2015), though as many pheasants would die before becoming fully grown (Sage *et al.*, 2018), this figure could be lower.

The common pheasant's natural range stretches across much of Asia but has now been extended across the globe for its use as a game quarry, with confirmed records in the UK from the 11th century (Hill and Robertson, 1988b). Pheasants were not a primary gamebird in the UK until the 20th century, when a shift occurred away from the shooting of grey partridge (*Perdix perdix*) due to the ease with which pheasants could be captively bred. This change from supporting larger wild populations in favour of captive rearing and release marks the beginning of the commercial pheasant rearing industry and a change in traditional gamekeeping practices. Despite pheasants being present at low densities for many hundreds of years, the current extent of mass releases in the UK has the potential to place a significant burden on UK wildlife and ecosystems.

1.1.2 Captive rearing and the release pen system

Most pheasants released in the UK are reared from day-old chicks in large, heated sheds accommodating hundreds to thousands of chicks. These modern methods are far more efficient than traditional methods such as incubating eggs under a hen pheasant or bantam (Swarbrick, 1985). 'Rearing' itself covers the pre-release period comprising the first 6-7 weeks of a pheasant's life. After this, they are delivered to the shoots and 'released' into open-topped pens where they typically voluntarily remain for 4-6 weeks, typically during July and August. The quantities, locations, and timing of releases are subject to no legal regulation as pheasants are considered naturalised and non-invasive, meaning that management and release techniques can vary greatly between shoots.

Release pens are fenced-off areas of woodland designed to acclimatise captive-reared pheasants to the wild. Where possible, pens have mixtures of habitats comprising sunny open areas for feeding and socialising, low 0-1m ground vegetation to encourage foraging, relatively dense 1-2m shrubby cover to provide protection from predators and encourage roosting, and trees that enable roosting (Game and Wildlife Conservation Trust, 2008). Hoppers filled with either grain or high protein crumb provide most of the bird’s nutrition, as release pens are far too small to support sufficient forging. Very often the pheasants have their wings clipped prior to release, inhibiting their capacity to fly from the pen until the feathers are regrown (Game Conservancy, 1996). This allows gamekeepers to ensure that the pheasants stay within the confines of the release pen for an average of 4 weeks, after which they can either fly out or the keeper opens the pen, enabling the pheasants to move outside during the day and return to the pen’s relative safety at night (Bicknell *et al.*, 2010). Pens are usually placed in areas that reduce the likelihood of pheasants dispersing away from shot land but are also constricted by the available habitat (Hill and Robertson, 1988b). As pheasants are acclimatising to the wild environment within the confines of the release pen, they forage, socialise, feed, and produce waste (Hill and Robertson, 1988b), all of which can disturb and damage the habitat within the pen. Stocking densities of 700 pheasants/ha of release pen should reduce potential negative impacts upon the release environment caused by ground disturbance and foraging behaviours (Sage and Swan, 2003), but average stocking densities have been shown to be as high as 2250 pheasants/ha (Sage, Ludolf and Robertson, 2005), with some pens almost double this. Once the pheasants are outside the pen, grain hoppers are strategically placed around shot land to minimise bird dispersal by providing ready food sources.

1.1.3 Reducing pheasant release numbers and how that relates to this thesis

Reducing the numbers of captive-reared pheasants that die naturally or fail to contribute to population growth means that fewer birds could be released, yet the same numbers could be harvested. To this end, novel method of improving the quality of pheasant welfare during rearing have shown promise at improving post-release survival, which in turn can lead to smaller releases. The methods of improving diet (Whiteside, Sage and Madden, 2015) and providing perching material (Whiteside, Sage and Madden, 2016; Santilli and Bagliacca, 2017) have the potential to be tested under commercial pheasant rearing conditions instead of smaller scale experimental rearing, but this in itself produces four key issues. First, can these methodologies be worked into the much larger and more intensive scale of commercial pheasants rearing, and if so, do they produce the same benefits in a cost-effective manner over a variety of sites? Second, in what additional ways might enhanced rearing affect the morphology and behaviour of pheasants raised in this way? Third, what impact might these changes to the pheasants have from the hunter's (hereafter referred to as 'guns') perspective? Finally, will enhanced rearing lead to unforeseen impacts on the environment within which the pheasants are released? It is these questions that the core of my thesis will endeavour to answer. Additionally, to efficiently analyse how changes to pheasant rearing practices are affecting harvest rates and pheasant populations as a whole, robust monitoring method must but used. Therefore, any study looking at changing aspects of pheasant release or management should adopt the following approach – evaluate intervention success; estimate economic costs and benefits; search for potential non-economic consequences for humans (guns and shoot managers) and the environment; consider long term effects; confirm that survey methods are robust. The following sections of this chapter will present pheasant releases in a wider context and how the above research aims could provide a positive impact on pheasant releases in the UK.

1.2 The positive and negative aspects of pheasant releases

1.2.1 Overview

In the UK, shot land is highly managed to accommodate pheasants. Management designed to maximise pheasant harvests can have beneficial knock-on effects for other wildlife while some practices can have mixed or adverse effects. In a review of the costs and benefits of gamebird shooting (of all quarry species) across Europe, Mustin et al's (2018) found a mixed picture. On average, direct effects of gamebird releases are negative, such as disturbance of habitat within release pens, predation of larger invertebrates, and degradation of the hedgerows close to release pens. Positive aspects of pheasant releases for wildlife tend to come indirectly as spill-over from practices carried out to support pheasant populations, such as habitat management, the removal of land from intensive agriculture for use as game cover, and supplementary feeding for pheasants providing additional food sources for other animals. In order for pheasant releases to have a net gain for wildlife, the negative aspects, often driven by high density releases (Sage, Ludolf and Robertson, 2005; Sage *et al.*, 2009; Neumann *et al.*, 2015; Capstick, Sage and Hoodless, 2019), must be reduced whilst the positive aspects are retained. The main impacts of pheasant releases will now be broken down into largely positive or negative categories, although such effects can vary greatly between sites and release sizes.

1.2.2 Positive effects of pheasant releases

1.2.2.1 Positive effect on woodlands

Roughly 500,000ha of woodland in the UK are managed for game shooting, with 100,000ha of that being copses maintained as a shelter for game (PACEC, 2014). Large areas adjacent to release woodlands are often removed from agriculture and planted with cover crops to provide additional shelter, movement corridors, and to fosters pheasants' natural instincts to forage and feed (Draycott, Pock, & Carroll, 2002). Management carried out by gamekeepers accounts for 3.9 million work days of active conservation for UK habitats (PACEC, 2014), and species that share these habitats gain from the nearly 2 million ha of land that is actively managed for game (PACEC, 2014).

The woodland in areas managed for game-shooting can be considered to be in better condition than other woodland. Woodlands managed for pheasants have 2%-7% less canopy, causing a denser understorey of between 5%-58% more ground vegetation. This may explain the 32% increase in bird numbers found in such woods, with woodpigeons (*Columba palumbus*), warblers, finches, and ground feeders being more abundant (Draycott, Hoodless and Sage, 2008; Bicknell *et al.*, 2010). Pheasant release woodlands also contain significantly higher numbers and more species of butterflies than unmanaged woodlands or those used for commercial forestry, likely because of higher levels of sunlight that penetrate the canopy (Robertson, Woodburn and Hill, 1988; Bicknell *et al.*, 2010). However, such benefits are not universal, with some sites showing little difference in invertebrate populations between woodlands managed and unmanaged for pheasants (Davey, 2008). Pheasant management can also encourages the creation of habitats of conservation concern such as hazel coppices, which support animal species of conservation concern such as dormice (*Muscardinus avellanarius)* (Bright and Morris, 1994).

One particular feature of woodlands manged for game-shooting may be especially beneficial. Rides, strips of woodland cleared to create a proxy for woodland edges to attract pheasants, comprise on average 13% of woodlands managed for pheasant, compared to 8% of non-pheasant woodlands (Game and Wildlife Conservation Trust, 2016). Responsible creation and maintenance of rides can provide large open glades in which species of non-shade-tolerant flora and light-loving fauna can thrive (Robertson, Woodburn and Hill, 1988; Draycott, Hoodless and Sage, 2008). Ride creation also encourages the development of woodland understory, a habitat that’s reduction has led to the decline of many woodland passerines (Fuller *et al.*, 2005).

1.2.2.2 Positive effect on arable land

Various arable management options to improve pheasant populations also have beneficial knock on effects for other wildlife, primarily through habitat creation and increased availability of food items.

Removing an area of land from agricultural use for a time, called set-aside, can be used to provide habitat and food sources for pheasant populations (Draycott, Pock and Carroll, 2002), but it also provides an important over-winter food source for other wildlife, with five out of six declining farmland bird species found in significantly higher numbers on areas with set-aside (Buckingham *et al.*, 1999). Beetle banks, isolated strips of sown tussock-forming grass located within arable fields, are also used as another method of providing cover and food for pheasants (Thomas, Goulson and Holland, 2001). They also provide areas of refuge and potential food sources within large arable fields for other wildlife such as grey partridge and corn bunting (*Emberiza calandra*) (Boatman, Stoate and Watts, 2000; Vickery *et al.*, 2004). Additionally, beetle banks can reduce numbers of aphids on winter wheat (Collin et al 1997), leading to reduced needs for pesticides. Decreased use of pesticides in general is also a proven method used for increasing gamebird brood sizes by increasing insect prey availability (Sotherton, Robertson and Dowell, 1993), and pesticide reduction can then have wide ranging benefits both for wildlife and human health (Pimentel *et al.*, 1991).

However, many farming management options that bring positive effects to both pheasants and other wildlife may only be adopted if a shoot is actively trying to increase the number of breeding pheasants or retains as many pheasants as possible after the shooting season (Hinsley *et al.*, 1999). With an estimated 83% of shoots relying solely on pheasants released that year (Bicknell *et al.*, 2010), there is far less drive for some shoots to instigate such beneficial measures, as the return on the investment is often outweighed by simply releasing more pheasants. This furthers the problems caused by high density releases.

1.2.2.3 Positive effects of predator control

Reduction of predator numbers, both avian and terrestrial, is a primary pheasant management technique used to reduce predation losses (Hill and Robertson, 1988b; Heydon, M.J. and Reynolds, 2000; Sage *et al.*, 2018; Porteus, Reynolds and McAllister, 2019), but it can also have positive effects for other wildlife. The red fox (*Vulpus vulpus*) is the pheasant's primary predator (Sage *et al.*, 2018), and as many ground-nesting birds are also predated by red foxes, the reduction of fox numbers to support gamebirds can also improve populations of other species (Angelstam, 1986;

Isaksson, Wallander and Larsson, 2007; Fletcher, Nicholas J Aebischer, *et al.*, 2010). This is particularly important when considering the national and global declines in ground-nesting and farmland birds (Isaksson, Wallander and Larsson, 2007). Currently, studies conflict on the level of impact of predators on other wildlife and the benefits from predator control. Fletcher et al (2010) showed a 3-fold increase to the breeding success of target bird species after predator control, Stoate and Szczur (2001) found that a general combination of game management techniques, including predator control, resulted in increased abundance of breeding passerines, but Thomson et al (1998) showed no correlation between the spread of avian predators and declines in songbird populations. The impact of predator control on other species is often driven by the initial densities of predators (Bolton *et al.*, 2007), so results can vary substantially between sites.

However, on shoots that care little for retaining previous years' pheasants and promoting the breeding populations of pheasants, much of the predator control is only carried out consistently between pheasant releases and the end of the shooting season (Bicknell *et al.*, 2010), meaning that during the spring, when prey are breeding and most vulnerable and predators are hunting at greater frequencies to support their young (Sargeant, 1972), there is often little if any predator control.

1.2.2.4 Additional positive impacts

Grain hoppers provided to feed pheasants also increase food availability for other wildlife (Draycott, Hoodless and Sage, 2008). Draycott (2005) found that only ~22% of hopper use is accounted for by gamebirds, with ~45% by passerines, ~18% by mammals, ~9% by columbids, and ~6% by corvids. Wood mouse (*Apodemus sylvaticus*) and bank vole (*Myodes glareolus*) populations have been shown to increase with proximity to feed hoppers (Davey, 2008), and gamebird feeders have been shown to be used by 47 different species (33 birds and 14 mammals), with 67% of the grain being eaten by species other than gamebirds (Sánchez-García, Buner and Aebischer, 2015).

Released pheasants also provide potential food sources for predators in winter, disrupting the usual predator-prey population dynamics (Korpimaki and Krebs, 1996; Roos *et al.*, 2018). For protected species, such as red kites (*Milvus milvus*), buzzards (*Buteo buteo*), and other raptors, this availability of additional food could be a potential boon for their populations, both by providing an ample food source and by reducing predation on other animals, delivering conservation benefits for struggling predator species. Bicknell et al (2010) hypothesise that the increase in pheasant releases has helped the reestablishment of buzzard populations in UK lowlands over the past 20 years, and the population numbers of generalist avian predators have been generally positively associated with increased gamebird populations (Pringle *et al.*, 2019). Shot pheasants that are not retrieved or that die by other means, such as the estimated 6% that are hit by cars each year (Turner, 2007), also provide additional food sources for scavengers, and gamebird carcasses left in the open are usually scavenged within 1.5-3.3 days after death (Pain, 1991).

1.2.3 Negative effects of pheasant releases

1.2.3.1 Negative effects on woodlands and hedgerows flora and fauna

The effects of pheasant releases on woodland and hedgerow fauna can be negative. Species such as tits, finches, and larks that are positively associated with dense hedgerows may be negatively affected indirectly by pheasant releases due to the detrimental effect they can have on hedgerow structure (Sage *et al.*, 2009; Bicknell *et al.*, 2010). Pheasant releases also impact invertebrate communities. High density pheasant releases (>1000 birds/ha of release pen) cause reductions in large carabids (>17.0mm) and those carabids that are active in spring within the release pen while also shifting the invertebrate community assemblage within the wooded release pens to more closely resemble that found on arable land (Neumann *et al.*, 2015). Areas where pheasants were released also had significantly less invertebrate biomass year-round and specifically reduced lepidoptera larvae biomass (Pressland, 2009), conflicting with the results that have shown gains that can be made by lepidoptera through efficient game woodland management.

Pheasant releases can also be detrimental to flora. In general, release pen interiors have increased bare ground, a reduction in vegetation below 50cm, and lower average species diversity (Sage, Ludolf and Robertson, 2005). Soil within the release pen is also altered chemically by the build-up of pheasant faeces increasing potassium levels (Sage, Ludolf and Robertson, 2005), causing knock-on effects to plant communities and the invertebrates they support. Although these changes may be limited to the release pen and the area immediately around it, many pheasant release pens are located within Ancient or Semi-Natural Woodlands (Sage, Ludolf and Robertson, 2005), a habitat that is of high conservation concern. Release pens are also often relocated to reduce disease likelihood and to provide fresh habitat that has not been degraded by the concentrated presence of pheasant. However, it can take over ten years for significant signs of recovery to the ground flora and soil chemistry to take effect after the pen has moved (Capstick, Sage and Hoodless, 2019), and this only occurred on sites with stocking density <1000 pheasants/ha. Negative effects on flora can extend beyond the release pen as well. Sage et al (2009) found that hedgerows within 250m of pheasant release pens, which are often used to facilitate movement, had increased bare ground, more weeds, fewer stable perennials, and fewer tree and shrub seedlings compared to hedgerows >500m away from release pens. They also found that although the hedge structure itself was not significantly different, the leafiness of the shrub layer was reduced. These negative effects were often, but not entirely, confined to hedgerows close to release pens that were stocked with >1000 birds.

1.2.3.2 Negative effects from increased predator populations and predator control

Releasing pheasants can support higher predator populations which may also predate non-gamebird, native wildlife. The percentage of pheasant in fox diet is positively correlated with pheasant densities (Ferrari and Weber, 1995), and the UK has higher generalist predator densities (e.g. red fox and crow) than other European countries (Roos *et al.*, 2018). This is likely in part due to our unique system of mass pheasant releases removing prey availability as a limiting population factor for large portions of the year (Webbon, Baker and Harris, 2004; Bicknell *et al.*, 2010). Between 34-81% of spring pheasant biomass is predated by foxes alone (Baker *et al.*, 2006), yet these levels are sustainable due to consistent pheasant releases. However, such additional influxes of population do not occur for other prey species. With released pheasant populations reduced to ~16% by spring (Turner, 2007), the increased number of predators brought about by pheasant releases will switch to other prey species, which could be particularly damaging to breeding ground-nesting birds (Angelstam, 1986). With regards to more direct negative impacts, the conflict, or perceived conflict, between gamekeepers and raptors leads to illegal predator control being carried out against raptors (Parrott, 2015), with Kenward et al (2001) finding that 10% of the 136 radio-tracked buzzards in their study were illegally killed in close proximity to pheasant pens. With all raptor species in the UK protected under law, any predator control against them is not only damaging to wildlife but also illegal.

1.2.3.3 Additional negative effects from pheasant releases

Released pheasants can pose a threat to native fauna through disease transmission (Tompkins *et al.*, 2002; Aebischer and Ewald, 2004). Static feed hoppers facilitate disease transmission via concentrations of infected faeces mixing with feed grain spilt on the ground below them (Gethings, Sage and Leather, 2015). Larger stocking densities and releases have been directly related to increased disease transmission for pheasants (Draycott *et al.*, 2006; Gethings, Sage and Leather, 2015), and mass pheasant releases facilitating greater transmission of parasites to grey partridge have been proposed as a caused for reduced grey partridge numbers (Tompkins, Draycott and Hudson, 2000); although this theory could not be replicated under lab conditions (Sage *et al.*, 2002).

The carcasses of dead and wounded shot pheasants may provide a very easy and beneficial food source for species that often scavenge, such as buzzards and red kites, but it also results in high levels of lead poisoning through ingestion of lead shot (Pain, Sears and Newton, 1995). Red kites were found to have elevated lead levels in 34% of sampled living birds, while 14% of dead birds were found to have lead at greater than lethal levels and 9% with lead as the probable cause of death (Pain *et al.*, 2007), and so a direct link can be made from pheasant shooting to the causes of death of this species of high conservation concern.

1.2.4 Conclusion

There are clear negative effects from pheasant releases, such as habitat and faunal degradation, supporting higher populations of predators, and lead poisoning in scavengers. The most damaging of the negative effects, such as habitat and faunal degradation, are more pronounced at higher density releases (Sage *et al.*, 2009; Gethings, Sage and Leather, 2015; Neumann *et al.*, 2015). One way that these negative issues could be removed would be to ban pheasant shooting altogether. However, this would not only cripple the £2 billion that the shooting industry adds to the UK economy each year but may also remove an economic incentive for retaining the vast areas of habitat excluded from intensive agriculture and the beneficial habitat management associated with it (PACEC, 2014). Another solution would be to continue with current practices. However, the yearly average 4.3% increase in pheasant release numbers (Aebischer, 2019) cannot be sustained indefinitely, if it even is sustainable currently. Another solution would be to ban releasing pheasants but allow for continued shooting of wild-bred pheasant populations. This option has some support, with the majority of gamekeepers being willing to shift their management practices from releasing pheasants to managing those naturally present in the landscape (Greenall, 2007), but this too would result in falls in the economic gains from shooting by drastically reducing the number of birds available to be shot and is an idea that is very unpopular to most within the shooting community (Greenall, 2007). Finally, restrictions could be placed on release numbers and release locations, reducing the negative effects of high-density releases but allowing shooting to continue at levels somewhat similar to current practices.

Although this final option may prove the most effective at balancing the benefits for wildlife with the wishes of those involved in shooting, currently there is no such legislation in place to implement it. As such, reducing the negative environmental aspects of gamebird releases within the current rearing and release system is the most viable option, and to do this, methods must be found that can facilitate reduced releases sizes without adversely affecting harvest rates. One way to achieve this is by reducing pheasant mortality post-release.

1.3. Why are so many pheasants released?

1.3.1 Pheasant release numbers

Traditionally, shooting on private estates and syndicated farmland was recreational. However, socio-economic changes over the past 50 years caused a dramatic increase in the number of ‘sold days’ and gave rise to entirely commercial shoots, drastically increasing the numbers of pheasants being released. As of 2010, 83% of shoots rely solely on released pheasants (Bicknell *et al.*, 2010), with the remainder being almost entirely small shoots with small shooting harvests (bag counts). On average, only 35% of released pheasants are actually shot, down from 50% between 1960-1990 (Robertson *et al.*, 2017), but the unharvested birds make little contribution to future year’s harvests. Turner (2007) recorded that only 16% of pheasants were still alive and within the vicinity of the shoot by the end of the shooting season, and often as little as 9% of released pheasants remain by the beginning of the breeding season in spring (Hoodless et al. 1999). Because of such losses and the increase in popularity of driven shooting, numbers of pheasants being release have steadily increased. However, the number of pheasants shot has not matched this increase since the early 1990s, with larger release numbers producing diminishing returns (Robertson *et al.*, 2017).

This loss and effective waste of unharvested birds has three detrimental effects. First, unharvested birds do not bring income to the shoot, so represent an economic cost. Ensuring an economically viable harvest requires that a certain number of birds must be shot. This is not due to the pheasant's value as meat, which is on average only £0.20-£0.30 per bird if the shoot is paid for the carcasses at all (Game and Wildlife Conservation Trust, 2018), but is instead due to the cost paid by those participating in shooting for every bird shot, averaging at £34.61 per bird (Game and Wildlife Conservation Trust, 2018).To achieve a profit in the face of predicted losses from causes other than shooting, shoot managers must release an excess of birds. Second, the release of excessively large numbers of birds, especially if released at high densities, can cause environmental damage as described in the previous section. Third, the loss of birds to a fate for which they were not intended (i.e. recreational harvest) represents an ethical cost, and opponents of shooting can rightly object to the needless waste of reared gamebirds.

As the primary cause for such large release numbers is high levels of natural mortality prior to the end of the shooting season, methods of improving survival must be found. This requires an understanding of the causes of such high mortality and an exploration of methods to try and reduce this, allowing for areas in which current methods can be improved or novel methods created to be identified.

1.3.2 Causes of mortality

With 35% of pheasants being shot (Robertson *et al.*, 2017) but only 16% surviving to the end of the shooting season (Turner, 2007), an estimated 49% die by other causes before or during the time when they could be shot. Natural mortalities are due to predation, disease, human action and starvation. Each of these factors has the potential to be moderated by management interventions.

1.3.2.1 Pheasant predation

Figures looking specifically at the UK release system put captive-reared pheasant mortality rates at 5.5% every 10 days for the first 30 days after release, 11.6% between 31-70 days, 6.0% between 70-240 days, and 2.3% between 241-365 days (Robertson, 1988). As predator numbers stay fairly constant throughout this period while pheasant numbers decline, this reduction in mortality hints at an acclimatisation to the wild environment by released pheasants so that they more closely match the seven times higher survival rates of wild bred pheasants (A. P. Leif, 1994). Predation, primarily by the red fox, is highest immediately after release (Frey *et al.*, 2003). Sage et al (2018) put average fox predation between release and the beginning of shooting (October) at 19.2 ± 4.0%, with a further 15.9 ± 1.9% lost during the shooting season. Predation levels are also increasing due to agricultural intensification increasing predation risks by reducing habitat that provides cover for pheasants while foraging, moving, and roosting (Taylor, Wolfe and Baxter, 1978; Warner, 1994). Birds of prey, particularly buzzards, also predate upon pheasants. Kenward et al (2001) found 5.6% of pheasant mortality was from birds of prey, with 4.3% from buzzards alone, but a larger meta-analysis by Parrott (2015) found that 90% of UK shoots lost <1% of their pheasants to raptor predation, with only extreme cases increasing to >5%. Reduced predator avoidance and ineffective roosting behaviour exhibited by captive-reared birds may explain their higher predation rates when compared to wild bred pheasants (Krauss, Graves and Zervanos, 1987; Hill and Robertson, 1988a). Captive-reared pheasants are less fearful of humans, more visible upon approach, and stay closer to the release site, creating a honey-pot effect of more visible prey for predators (Krauss, Graves and Zervanos, 1987; Hill and Robertson, 1988a; Robertson, 1988).

1.3.2.2 Disease

The spread of disease in reared pheasants poses significant problems for gamekeepers and pheasant breeders both during the rearing and release process and post-release (Goldová *et al.*, 2006). Parasites such as *Heterakis gallinarum*, *Capillaria* spp. and *Syngamus trachea* are commonplace in pheasant populations, particularly at high stocking densities (Draycott *et al.*, 2006), and parasitized pheasants breed less successfully and are more susceptible to predation (Millán *et al.*, 2002; Draycott *et al.*, 2006). The spread of diseases and parasites is far more prevalent in released pheasants than wild pheasants, as feed and faeces can mix easily both within the release pens and around hoppers placed about the shoot (Gethings, Sage and Leather, 2015), and often 100% of released pheasant populations are infected with *H. gallinarum* to some degree (Draycott *et al.*, 2000). As disease becomes a greater problem with increased releases densities (Gethings, Sage and Leather, 2015), it is often the largest shoots that are forced to increase their release numbers further to accommodate disease losses.

Within the rearing and release pens, average mortality from disease and parasites can vary greatly based on the speed of identification of an infected individual and application of medication. As an example of an extreme case, one shoot used as a study site in this thesis suffered losses of roughly 300 out of 500 pheasants within 3 weeks of release due to infection (likely with coccidiosis). Comparing this to another release in our project which saw 22 of 800 birds dying of various infections whilst in the release pen, we can see the inconsistencies and spikes of infection induced mortality.

1.3.2.3 Starvation

Captive-reared pheasants may also be lacking the skills to identify high-quality food items (Hoodless et al, 2001), affecting both their fitness and their ability to reproduce successfully. To some extent, the provision of feed hoppers can negate these deficiencies. However, outside of the shooting season, many shoots stop providing feed and force pheasants to rely on foraging to sustain themselves (Draycott *et al.*, 2005; Sánchez-García, Buner and Aebischer, 2015). Although pheasant densities are often of an order of magnitude lower after the shooting season (Turner, 2007), the poor development of pheasant foraging strategies might still adversely affect their survival and reduce the number of pheasants available to a shoot by the next shooting season. Beyond reducing body condition, inefficient foraging ability also increases the time spent foraging out of cover and the subsequent increase in predation risk (Whiteside, Sage and Madden, 2015). Availability of natural food sources in general also impacts pheasant survival, with pheasant populations positively affected by increased unharvested land, increased ‘useful' crops such as barley, and decreased use of pesticides (Coates *et al.*, 2017), but all of these practices have declined due to increases in agricultural intensification. A major impact that disease and starvation have upon pheasants once outside of the release pen is through reducing overall health and increasing the likelihood of other forms of mortality, primarily predation. As such, estimating mortality expressly due to starvation and disease is hard to quantify outside of the rearing and release pens.

1.3.2.4 Dispersal

Pheasants that disperse from shot land are effectively lost to that harvest. They may also be more likely to die, especially if they leave an area where predator control is carried out (Sage *et al.*, 2018). In the UK, intensive management and nationwide releases likely result in smaller levels of dispersal when compared to the other countries (Leif, 1994; Hoodless, Draycott, and Lundiman, 2001), and Turner (2007) recorded distance travelled by pheasants from the release pen ranging from 32m to 4685m prior to the shooting season in October. With many UK shoots taking place over relatively small areas, dispersal from release sites of just a couple of kilometres would mean those birds are no longer present on shot land and effectively lost to that shoot. However, dispersal can work both ways, with Turner (2007) reporting that 6% of shot pheasants from her study were immigrants, released from neighbouring shoots.

1.3.2.5 Survival differences between wild and captive-reared pheasants

Breeding animals in a controlled environment and releasing them into the wild is often used to supplement wild populations (Mathews *et al.*, 2005). However, the success of such releases is not assured, and individuals may fail to thrive because they do not behave appropriately for their environment due to abnormal early life rearing (Snyder *et al.*, 1996). The release of captive-reared pheasants is no different.

As wild and captive-reared pheasant exist in the same habitat and under the same management conditions, differences in survival likely result from some aspect of the rearing process (A. Leif, 1994). The primary method through which a lack of natural behaviours affects captive-reared pheasants is their reduced predator avoidance (Krauss, Graves and Zervanos, 1987). Captive-reared pheasants have similar mortality rates to wild pheasants in areas of naturally low predator densities (Kallioniemi *et al.*, 2015), suggesting that predation is a major discriminator between wild and captive-born birds. This can be seen in hen pheasants of wild stocks having survival rates 5-10 times higher than those of captive-reared stocks (Musil and Connelly, 2009). Declining mortality rates post-release suggest that, given time, pheasants will adapt and naturally learn these essential survival skills (Robertson, 1988), but mortality rates immediately after release are often still large (Krauss, Graves and Zervanos, 1987).

1.4 Methods for reducing wasted pheasants

1.4.1 Directly reducing predation

Both pheasant adult and chick populations increase in the presence of predator control (Sage *et al.*, 2018; Trauman et al, 1974; Jensen, 1970), and Sage et al's (2018) meta-analysis found average predation losses at estates with high predator control to be 30% ± 5.3% compared to 59% ± 4.7% at those with little predator control. However, such predator control must be carried out consistently and over large areas to prevent predator populations from quickly re-establishing (Chesness, Nelson and Longley, 1968; Frey *et al.*, 2003), and decreases in fox numbers through culling are often offset by the immigration of foxes from outside of controlled areas (Baker and Harris, 2006). Where direct predator control cannot be carried out, as is the case for raptors, non-lethal methods can be attempted. These include methods such as providing supplementary feed for predators, but these can often be either inefficient or very costly (Redpath, Thirgood and Leckie, 2001), limiting their use.

Predator control, primarily fox control, is already carried out widely where it is needed most, with the most foxes killed where the most foxes are present (Baker and Harris, 2006). As such, there is little scope for increasing it further without the persecution of protected species or the adoption of illegal predator control practices, such as use of poison bait.

1.4.2 Habitat and release management

Better release management can improve pheasant numbers both through improving their survival and reducing dispersal (Messmer and Rohwer, 1996). Such methods include regularly moving drinkers and feed hoppers within the release pen to reduce the likelihood of disease transmission (Gethings, Sage and Leather, 2015), increasing shrubby cover in release pens to reduce raptor predation (Kenward *et al.*, 2001), releasing pheasants later to reduce time exposed to predators and to reduce the time pheasants have to disperse (Thomas F . Haensly , S . Mark Meyers, 1985; Turner, 2007; Lloyd, 1976), and continuing to provide feed year round (Hoodless *et al.*, 2001; Draycott *et al.*, 2005). Lowering release pen stocking densities reduces dispersal and lowers the likelihood of disease outbreaks and feather-pecking (Sage and Swan, 2003; Turner, 2007), but lower release densities would mean increasing release pen areas in order to maintain current harvest levels, resulting in increased costs to shoots and further spreading the negative environmental effects associated with release pens (Sage, Ludolf and Robertson, 2005). Most shoots compensate for disease risk by medicating their pheasants, but this becomes significantly harder once the pheasants disperse beyond the release pens (Mcquistion, 1987).

Most commonly used pheasant management techniques aim to improve habitat availability and quality during the autumn and winter (Hill and Robertson, 1988b), as it is simply more cost-effective to support the masses of pheasants released in summer than support small numbers of wild or surviving birds after the shooting season. Heterogeneity in available habitat types has been shown to benefit pheasant populations (Whittingham & Evans, 2004; P. A. Robertson et al., 1988), with particular benefits of increasing woodland edge area (Game Conservancy, 1988). Planting game cover crops adjacent to woodlands offers shelter, easy paths of movement, fosters predator avoidance, encourages foraging behaviours, concentrates pheasants to allow for more efficient shooting, and when combined with supplementary feeding, can further reduces dispersal (R. Draycott et al., 2002; Turner, 2004). However, in the UK where potential habitat space is in high competition with agriculture, habitat creation and planting extensive networks of game cover are often simply not viable. Although less intrusive methods, such as the recovery of marginal lands and alternate farming practices, have the potential to benefit pheasant survival (Clark and Diamond, 1993), the cost of such methods often severely curtails their potential benefits. In short, as with the maximisation of current predator control practices, most shoots are already maximising what land they can feasibly commit to habitat improvement instead of agriculture, meaning that additional methods of increasing pheasant survival and harvest efficiency must be found

1.4.3 Pre-release techniques

The fact that wild-born pheasants living alongside released birds within the same landscape and under the same management can survive seven times better (A. Leif, 1994) implies that the cause of these survival deficiencies occurs prior to release. Captive-reared pheasant chick survival matched that of wild stocks when the two were hatched and reared together (Thomas et al, 1985), showing that any genetic difference between the two groups, at least at the time of that particular study, had a negligible effect on survival. The artificial rearing environment is lacking natural stimuli that the wild birds receive (Whiteside, Sage and Madden, 2016), and so it may be possible to add natural elements to captive rearing environments to better mimic wild rearing and increase survival to more closely match that of wild pheasants.

Inducing more natural behaviours prior to release has been shown to be beneficial to gamebirds (Ferretti *et al.*, 2012). Breeding pheasants in the historical manner of using their mother or a mother surrogate leads to the development of better predator avoidance behaviours and increased survival post-release (Dowell, 1989; Ferretti *et al.*, 2012), but changes in economics, technology, and the expansion of the shooting industry have led to almost all captive-reared pheasants being raised at an industrial scale in sheds of hundreds or thousands, separated from their mothers or sitting bantam hens (Beani and Dessi-Fulgheri, 1998). Pre-release training techniques, such as early exposure to predators or predator models, have also been shown to reduce predation post-release (Miller *et al.*, 1990; van Heezik, Maloney and Seddon, 1999). However, the cost and time required to implement such techniques at the industrial scale are not feasible when simply breeding and releasing more pheasants is cheaper, meaning that different and simpler methods of improving the fitness of captive-bred pheasant must be considered.

Altering a chick’s early diet by adding a mixture of natural seeds and live invertebrates increases post-release survival by modifying their morphology and behaviour (Whiteside, Sage, & Madden, 2015). Whiteside, Sage, and Madden

(2015) provided a more natural diet to pheasant chicks from 1-day-old to seven-weeks-old, consisting of 5% mixed seed and fruit with 1% live mealworm in addition to the 94% of standard chick crumb. After one year, the number of pheasants from the improved diet group still alive was more than double that of the control group. This was attributed to birds reared with a more naturalistic diet being: more efficient foragers which allowed them to spend more time on vigilance behaviours, being better able to handle live prey, being less reliant on supplementary feeding which is not always available, and developing a more natural gut morphology. This experiment shows that relatively simple changes to the pheasant rearing diet can lead to more than twice as many pheasants being recorded over a year after release. However, this research was carried out at a relatively smaller scale, and not at the harsher, more industrial scale that dominates commercial pheasant rearing in the UK. Commercial pheasant rearing occurs at high densities similar to the manner in which broiler chickens can be raised, meaning aggressive behaviours and the detrimental effects that they can have on fitness occur at higher rates (Nicol *et al.*, 1999; Kjaer, 2004).

Environment enrichment of captive-reared animals via the provisioning of natural materials prior to release can improve both fitness and natural behaviours (Shepherdson, 1994), and this has also been shown in gamebirds (Miller et al, 2006). For pheasants specifically, Whiteside, Sage, and Madden (2016) added perching material into hand-reared pheasant pens during the first seven weeks after hatching, effectively shifting the rearing pen environment from two-dimensions to three-dimensions. This provoked a succession of morphological, cognitive, and behavioural changes that resulted in decreased post-release mortality. This result was due to three factors. First, perch-reared birds were morphologically better adapted to perching off the ground for longer due to thicker tarsus bones, reducing vulnerability to ground predators. Second, they were more likely to roost off the ground at night (although this difference between treatment and control birds declined over time post-release), producing the same effect. Third, the pheasants had better spatial working memory, likely allowing them to move more efficiently and thus spend less time at risk of predation. A similar investigation by Santilli and Bagliacca (2017) also found that pheasants provided with perching material during early life had a greater tendency to roosted off the ground in addition to reduced plumage damage compared to those reared without perching material. Although carried out at relatively small scales thus far, adding perching material and improving diet are novel pre-release interventions that have the potential to be easily transposed to mass pheasant rearing and could have significant benefits to reducing the high levels of captive-reared pheasant mortality if the benefits are still present under commercial rearing conditions.

1.5. Additional potential effects of rearing pheasants under enhanced conditions

1.5.1 Changes to body condition

Instilling more natural behaviours within Enhanced pheasants will likely also lead to morphological changes. In both of Whiteside, Sage, and Madden’s (2016; 2015) studies, changes to morphology were recorded, with perching material producing heavier birds with thicker tarsi while improved diet showed an altered gut morphology. These changes may be caused by either the adoption of new behaviours, such as increased roosting, or by differing nutrient uptake via an altered early-life diet. As such, recording and analysing morphological changes in pheasants will enable a clearer understanding of mechanisms explaining changes in survival and shooting as a whole. This will be achieved by identifying morphological characteristic that could be caused from behaviours that affect survival, such as thicker tarsi indicating a greater propensity to roost (Whiteside, Sage and Madden, 2016). Additionally, changes to body condition might also impact the pheasant meat industry, with greater or less quantities of meat present on Enhanced birds, providing another reason to investigate such potential changes. Changes in morphology will most effectively be investigated by carrying out post-mortem examinations of birds reared under Enhanced and Control methods and comparing the two.

1.5.2 Changes to pheasant flight performance

Improving pheasant fitness and body condition might not only alter survival but also impact flying ability. Enhanced Rearing aims to permit captive-reared pheasants to develop more like wild pheasants, and wild birds also fly higher and for longer than their heavier captive-reared counterparts (Robertson, Wise and Blake, 1993). It follows that improving early rearing conditions could then alter the body condition of captive-reared pheasants to make them closer to those of wild stocks, leading to better flying birds. As such, flight ability of Enhanced and Control birds should also be investigated. Pheasants that fly higher are also thought to be shot at a higher rate due to a preference by the guns to aim for harder targets (Robertson, Wise and Blake, 1993). This could mean rearing enhancements also have the potential to not only improve pheasant survival, but also the ‘quality’ of birds presented to the guns. However, this could also mean that higher flying birds’ contribution to harvests is skewed. This could result in disproportionate harvest rates between Enhanced and Control pheasants that do not accurately reflect increases in survival. As such, the effect of flight performance on likelihood of being shot should also be investigated.

1.5.3 Impact on surrounding wildlife

Pheasants are capable of eating a wide variety of foods, such as seeds, grains, berries, green shoots, arthropods, molluscs, and even small vertebrates (Hill and Robertson, 1988b). Enhancement of early rearing diet has been shown to reduce foraging times and decrease the time taken to catch novel invertebrate prey (Whiteside, Sage and Madden, 2015). This could be detrimental to the invertebrate populations within those environments. Possible effects will likely be concentrated within pheasant release pens, where pheasants will be at their highest densities, but Neumann et al (2015) found that pheasants show few significant impacts upon woodland invertebrate communities within their pens over the long term. However, releasing thousands of Enhanced pheasants with superior foraging capacities may change this, potentially causing reductions to invertebrate abundances due to increased predation or increasing degradation to the pen habitat from increased foraging behaviours above that which traditionally reared pheasants already cause (Sage, Ludolf and Robertson, 2005). Differences between the pen environment and that of the surrounding woodland might be most pronounced immediately following releases, when pheasants have not yet dispersed and are concentrated within the pens. Therefore, the effects on resident invertebrate communities by birds reared under Enhanced conditions should be investigated at this time.

1.6. Measuring changes in pheasant population demographics

1.6.1 The importance of determining pheasant population demographics.

Recording changes in pheasant populations is essential for both research and shoot management. Traditionally, shoots simply count the number of shot birds and compare this to release numbers to create an overall return percentage (Hill and Robertson, 1988b), but this provides no information for which pen the birds were released from, if they were even released on that shoot, or the age of those birds. Without this information it is very difficult to measure the effects of changes in management and release practices, reducing both a shoot's ability to reduce wasted pheasants and a researcher's ability to carry out most forms of detailed analysis. This is particularly relevant when trying to reduce release number by increasing year-to-year survival of un-shot pheasants and supporting larger wild breeding populations.

1.6.2 Methods and issues of measuring pheasant population demographics

A simple and cost-effective method to gather population demographic data is via tagging, such as the patagial tagging carried out for the Game and Wildlife Conservation Trust's National Game-Marking Scheme (NGMS) (Game and Wildlife Conservation Trust, 2019). Tags can be dated and made individual to each release pen, allowing for a more accurate accounting of what was shot and from where for both shoot managers and researchers. Patagial tagging in particular can be conducted en masse in a cost-effective manner and is the most viable method for determining numbers of Enhanced and Control birds in the harvest for this thesis if the tags remain undamaged (Carver, Vincent A, Burger, Loren W., Brennan, 1999). However, my initial work for this thesis found an estimated 36% of the ‘Multi-Tags’ used by both myself and the NGMS were damaged beyond use for subsequent years after 6 months, preventing the identification of mature birds in the harvest. Also, by extrapolating figures, potentially 20% of the Multi-Tags may have been lost entirely by the end of the first shooting season, leading to reduced tag records and inflating the results of pheasant wastage. As such, a more reliable form of patagial tagging than the commonly used Multi-Tags should be investigated and the rate of Multi-Tag deterioration should be investigated to correct past and future results.

Increasing the number of pheasants surviving between years and strengthening the wild population can also help reduce future release numbers, but in order to understand what contribution older pheasants make the to the harvest and assess the age demographics of the wild population, accurate methods of aging pheasants in the absence of tagging are required. This is particularly relevant for determining the effectiveness of, and increasing the efficiency of, specific management options designed to improve year-to-year survival and breeding success in the wild, such as predator control that can significantly reducing nest predation (Draycott *et al.*, 2008) and supplementary feeding which can increased breeding success (Draycott *et al.*, 2005). When tagging is not possible, either because the birds were wild-born and/or never tagged or the tags have fallen off, the collection and analysis of biometric data can be carried out to age pheasants (Woodburn *et al.*, 2009). Such biometrics include; body weight, tarsus length, head length, spur length, ratio of body weight to tarsus length and head length, the depth of the Bursa of Fabricius, and proximal primary feather length and diameter, and considering a mix of biometrics can be used to accurately classify 83% and 94% of the juvenile and mature pheasants respectively. Such biometrics provide a high degree of accuracy in classification, but their collection requires specialised skills and takes time, limiting data collection to specialists. However, the length and diameter of the proximal primary feather alone have proven to be accurate predictors of pheasant age if a known-age subsample can be used to calibrate juvenile and mature (pre and post first breeding season) feather metrics, resulting in 92% accuracy when classifying the ages (Greenberg, Etter and Anderson, 1972). This method is known as the Proximal Primary Method (PPM). Taking the proximal primary feathers alone has the potential to be widely used, as after collecting a range of biometric data to correctly age the calibration sub-sample, just the feather alone can be taken from additional birds. This would allow for extensive and swift data collection by non-specialists, greatly increasing the scope of data collection. However, one additional feather metric that has not been tested to see if its addition could improve the accuracy of PPM is the mass of the feather. The addition of this variable may further improve the accuracy of PPM and allow for more precision for both research outcomes and management decisions made based on aging pheasant populations via PPM.

Machine learning is an analytical technique that is offering novel approaches in data analysis over traditional methods by considering multidimensional metrics and non-linear relationships. This method is becoming widely used in ecology to categorise animals based on specific criteria (Larrañaga *et al.*, 2014), and allows for multiple machine learning algorithms (MLAs) to be swiftly and directly compared to identify which methods best increase predictive accuracy (Acevedo *et al.*, 2009). As such, it holds potential to improve upon the accuracy with which current PPM methods classify the age of pheasants.

1.7. Thesis overview

Chapter 2 of this thesis will test the viability of altering the commercial pheasant rearing system currently employed in the UK by adding improved diet and perching material to improve pheasant survival through the immediate shooting season and then that of the following year, with the intention that Enhanced Rearing could lead to increased pheasant survival, facilitating equal or greater harvest rates, yet requiring smaller releases sizes and reduced wastage within the current pheasant release system. It will also be necessary to assess whether these methods are cost-effective, a factor that will be essential if these methods are to be adopted by the pheasant rearing industry. Chapter 2 will also assess changes to morphology caused by the enhancements to further understand what, if any, impacts Enhanced Rearing has on pheasants.

Chapter 3 will study the flight performances of Enhanced and Control birds to further investigate the effects of Enhanced Rearing and identify any additional impacts that it might have on the shooting industry from the perspectives of those who shoot (the guns). Additionally, we will investigate if the flight performance of a pheasant influences the likelihood of it being shot, and if the flight performance of the pheasant population as a whole changes over the course of the shooting season.

Chapter 4 will investigate the overall impacts that traditionally reared pheasants have on invertebrate populations and habitats within the release pens. This will be used to both further present knowledge and as a benchmark to investigate if the presence of Enhanced pheasants alters these impacts, allowing further analyse of the effects of Enhanced Rearing and allowing for more informed recommendations for its adoption should it prove successful at increasing harvests. We will also investigate the effect that pen stocking density has on invertebrates and habitats within and around release pens and the chronic effects upon invertebrates and habitats caused by successive releases.

Chapter 5 will assess the effectiveness of monitoring pheasant population using patagial tags. Specifically, we shall compare the durability of the commonly used Multi-Tag patagial wing tag against a more durable tag type. Through this, we will develop a correction factor that can be applied to previous and future studies that use Multi-Tags, aiding in producing more robust datasets for both shoots and other research projects.

Chapter 6 will investigate the accuracy of aging pheasants based on the established method of analysing the length and diameter of the proximal primary feather and extend these by incorporating feather mass and using machine learning to attempt to improve classification accuracy.

This thesis will aim to explain the consequences that Enhanced Rearing might have with reference to the ecological, economic, and recreational aspects of the pheasant shooting industry. It is the hope of this PhD to find a method of reducing pheasant release numbers without adversely affecting either the benefits gained to wildlife by effective shoot management or the livelihoods of those involved within the shooting industry. This work will be of interest both to those in favour and against shooting, as improving sustainability and reducing the negative environmental aspects brought about by high density releases is an issue both sides wish to see addressed.

Chapter 2: Can adding dietary and pen enrichment improvements to a commercial pheasant rearing environment lead to increased pheasant harvest?

Abstract

Rearing pheasants under modern commercial conditions can lead to deficiencies in natural behaviours, causing higher rates of natural mortality. By improving rearing conditions to more accurately match those of wild-bred pheasants, post-release mortality rates of captive-reared pheasants could be reduced, resulting in more pheasants contributing to the harvest and necessitating smaller release sizes. Small-scale experimental studies have shown that providing perching material and a more natural diet can increase pheasant survival, but this work was carried out under very controlled conditions at single sites. Therefore, we combined both methodologies within a commercial pheasant rearing system to rear Enhanced pheasants, released them alongside traditionally reared Control pheasants, and measured their contributions to the harvest of 8 shoots.

Enhanced pheasants were harvested at a higher rate than Control, but this increase was inconsistent between sites. Enhanced birds were harvested at rates ~16%-17% higher on Large (>2000) and Small (<601) sized pheasant releases but ~6% lower on while Medium (601-2000) releases. When release date and not release size was considered, shoots that released prior to August 22nd harvested proportionately more Enhanced birds, but those that released after this point harvested proportionally more Control. Enhanced harvests increased over Control by 1.44% with every day prior to August 22nd that pheasants were released. Enhanced pheasants had proportionally larger breast muscles (+7.3%), hearts (+4.5%), and tarsi diameter

(+6.2%) and gained 0.82g of weight less each day after release than Control birds, but breast muscle and tarsus diameter increases were only present when Enhanced harvest rates were higher than Control.

Enhanced Rearing only increases the cost of rearing by roughly ~2.4% per bird, making it cost effective on Large and Small shoots or those that release earlier, resulting in fewer pheasants needing to be released to achieve the same harvest rates.

2.1 Introduction

An estimated 39-57 million pheasants (*Phasianus colchicus*) are released for shooting each year in the UK (Aebischer, 2019). The numbers of released birds actually being shot has declined over time, with the ~50% shot in the 1990s reducing to ~35% in 2005 (Robertson *et al.*, 2017), though since 2005 the fall in efficiency has been much slower. A major cause of such low harvest numbers (return rates) is that many pheasants die of natural causes prior to and during the shooting season (Hill and Robertson, 1988b; Sage *et al.*, 2018). Predation is the primary cause for this mortality, with fox predation alone accounting for 19.2 ± 4.0% of mortality prior to the shooting season and another 15.9 ± 1.9% during it (Sage *et al.*, 2018). Reducing these losses could permit shoot managers to release fewer pheasants yet harvest a similar number of birds. This could have several wide-ranging effects.

Firstly, there are environmental benefits. The release of increasingly high densities of pheasants can have negative effects on the surrounding wildlife, with increased damage to the environment in and immediately around the release pens (Sage, Ludolf and Robertson, 2005; Sage *et al.*, 2009; Capstick, Sage and Hoodless, 2019), declines in some bird and invertebrate populations in release woodlands (Draycott, Hoodless and Sage, 2008; Neumann *et al.*, 2015), and increased pheasant populations potentially increasing predator abundances (Pringle *et al.*, 2019) that could then increase predation pressures on other prey species (Roos *et al.*, 2018). Releasing fewer birds would limit such negative effects. Secondly, there would be economic benefits to shoot managers. The cost of rearing each pheasant is on average £12.41 per bird (Game and Wildlife Conservation Trust, 2018). The loss of each pheasant to a fate other than shooting is felt monetarily by shoots and contributes to both rising costs to those that carry out the shooting (collectively called ‘guns’) and losses to the shoots themselves, resulting in 42% of commercial shoots making a loss in 2017/2018 (Game and Wildlife Conservation Trust, 2018). Increasing pheasant survival would reduce these monetary losses. Thirdly, increasing survival may have ethical benefits. The raising of so many pheasants under artificial conditions, specifically for sport shooting, is already a major point of contention for some (Humphreys, 2010), and the fact that many more pheasants must be released to compensate for losses to natural predators rather than to fulfil the purpose for which they were intended (i.e. providing sporting targets and harvested food) increases ethical concerns.

Management methods to improve pheasants survival post-release typically focus on the landscape into which the birds are released through supplementary feeding, habitat management, and predator control (Draycott *et al.*, 2005; Sage *et al.*, 2018), but the high losses persist even with these methods in place. In their absence, losses would likely be even higher, with pheasant losses from predation found to be 29 ± 4.7% higher on ground with no predator control (Sage *et al.*, 2018). As such, novel methods for improving pheasant survival must be found. Additionally, methods such as predator control are also ethically contentious, despite being shown to produce net gains for other wildlife (Tapper, Potts and Brockless, 1996; Fletcher, Nicholas J. Aebischer, *et al.*, 2010). Alternatively, or additionally, improvements in pre-release management have the potential to improve pheasant’s post-release survival.

Pheasants may survive poorly after release because they have been reared under unnatural conditions, and this may detrimentally affect their development both physically and behaviourally (Brittas *et al.*, 1992; Sage *et al.*, 2003). Improving rearing conditions for captive-bred animals is an important aspect of improving post-release survival of animals (Mathews *et al.*, 2005), and an absence of features that mimic an animal's natural habitat within the rearing environment, such as perches and foraging spaces, can reduce the development of behavioural and physiological traits seen in their wild counterparts by depriving the animal of natural stimuli (Mathews *et al.*, 2005). Wild pheasants can have survival rates ranging from 74% to 700% higher than their pen-reared counterparts and breeding success from 200% to 500% times higher (Hill and Robertson, 1988a; Brittas *et al.*, 1992; A. P. Leif, 1994). This poorer survival and breeding success in pen-reared birds is largely caused by deficiencies in foraging, roosting, predator detection, and nest-siting behaviours that are likely induced by the commercial rearing environment (Krauss, Graves and Zervanos, 1987; Hill and Robertson, 1988a, 1988b; Sage, Robertson and Wise, 2001). These findings have stimulated a series of recent studies that attempt to reduce these negative effects by adjusting the rearing environment to produce pen-reared pheasants that more closely resemble their wild counterparts (Whiteside, Sage and Madden, 2016; Santilli and Bagliacca, 2017).

A paucity of roosting behaviours increases vulnerability to terrestrial predation in other released Galliformes, such as grey partridge (*Perdix perdix*) and cheer pheasants (*Catreus wallichii*) (Dowell, 1990; Garson, Young and Kaul, 1992), and the absences of roosting material within the pheasant rearing environment means that there are limited, if any, opportunities for them to develop perching behaviours and the associated morphologies during the first 6-7 weeks of their lives. To counter this, Whiteside, Sage, and Madden (2016) increased the probability of young pheasants using elevated perches to roost by adding perching material to the standard bare rearing environment. They found that this reduced mortality, enhanced morphological characteristics better suited to roosting, increased the rate at which the pheasants roosted, and improved their spatial memory. Similar research by Santilli and Bagliacca (2017) found that the provisioning of perching material led to higher rates of roosting off the ground once the pheasants were moved to release pens and lower rates of plumage damage caused by feather pecking.

Presenting food in a more natural manner improves captive-bred animal fitness by reducing abnormal behaviours and improving manual manipulation of dietary items (Shepherdson *et al.*, 1993; Kerridge, 2005; Regan and Kitchener, 2005), and improving foraging efficacy reduces predation by increasing vigilance behaviours, body condition, and fitness (Draycott *et al.*, 1998; Watson, Aebischer and Cresswell, 2007). Whiteside, Sage, and Madden (2015) incorporated these benefits into pheasant rearing by adding the weight of 1% live mealworm and 5% wild birds seed mix to commercial pheasant feed provided during rearing to facilitate a more natural diet. The provision of a more complex/varied diet resulted in pheasants spending more time being vigilant, increased their ability to handle live prey items, supported the development of a more natural gut morphology, and made the pheasants less reliant on supplementary feed. This method did not increase the harvest rate of pheasants on the year of release but did increase survival after the shooting season, but in other studies, techniques that also promoted better foraging have predicted more immediate increases in post-release survival in both captive-reared grey partridges and whooping cranes (Kreger *et al.*, 2006; Homberger *et al.*, 2014).

These manipulations of early rearing environments were all conducted at small scales at single study sites, but for these simple alterations to be adopted by commercial scale pheasant rearers they must satisfy three concerns from the shooting industry. First, they must deliver improved rates of survival and harvest across a range of sites and under commercial rearing conditions. When pheasants are reared under commercial conditions it is at high densities, with broiler chickens being an accurate comparison. This means that commercially reared pheasants may undergo some of the more negative aspects of high density rearing, such as increases in aggressive behaviours and the detrimental effects that they can have on fitness (Nicol *et al.*, 1999; Kjaer, 2004), such as reduced plumage quality, higher proportions of skin injuries, and increases beak-inflicted injuries (Kjaer, 2004). Second, shoot managers must be convinced that the altered rearing does not induce unforeseen changes that may be detrimental to shoots. Third, the benefits must be cost-effective in terms of the number of additional pheasants shot. The effects of improved rearing conditions might also differ depending on the shoot they are released at. Examples could be that earlier releases could lead to greater rates of dispersion and longer exposure to predators, and larger releases are more likely to be found on commercial shoots with full-time game keepers and greater investments in habitat management. It is essential to identify if any such differences between shoots affects the harvest rate of birds reared under improved conditions before recommending if and to where they are released.

Additionally, changes to the rearing procedures may bring unexpected detrimental economic consequences for the shoot purchasing and releasing the birds. First, early-life exposure to an enriched diet may make released pheasants less reliant on the feed provided by shoots (Whiteside, Sage and Madden, 2015). This could facilitate greater dispersal and lead to fewer pheasants being available to be harvested, despite increase survival, if they move away from the shoot where they were released. Of course, these birds may be shot elsewhere, but this provides no compensatory revenue to the shoot that purchased them. Second, alterations to the body condition of the birds may affect their desirability for game dealers and butchers. Wild pheasants are lighter than their pen-reared counterparts (Majewska *et al.*, 1979), but providing perching material produced pheasants that were heavier for both Santilli and Bagliacca (2017) and Whiteside, Sage, and Madden (2016). If rearing Enhanced pheasants does impact mass, it could in turn impact the pheasant meat industry and the desirability and value of harvested pheasants. Access to perches has also been shown to increase tarsus thickness (Whiteside, Sage and Madden, 2016; Santilli and Bagliacca, 2017). Both the differences in weight and tarsi were removed several months after release (Whiteside, Sage and Madden, 2016), implying that some differences caused by providing perches are only temporary, likely from non-perch birds developing their own perching behaviours and associated morphological changes after significant time exposed to the wild environment. However, measuring these and other potential morphometric changes (such as breast muscle, heart, and body fat) may provide a good indicator that rearing improvements are having an effect beyond basic harvest rates and also indicate what might be causing potential effects on survival.

In this chapter, we extended work by Whiteside, Sage, and Madden (2015,2016) and Santilli and Bagliacca (2017) by combining the provisioning of perching material and improved diet into what shall now be referred to as the Enhanced Rearing methodology. We then applied these techniques to pheasants reared under commercial conditions and released them over a range of shoots. These Enhanced pheasants were tagged and released into each pen alongside the same number of traditionally reared tagged Control pheasants to standardise all variables outside of the rearing environment, allowing for a direct comparison between the two. The two specific questions this chapter investigates are 1) does Enhanced Rearing improve pheasant harvests? and 2) How does Enhanced Rearing affect pheasant morphology and attendant behaviour and carcass properties, and can these alteration help explain the effects of Enhanced Rearing on survival?

2.2 Methods

2.2.1 Rearing and tagging

Rearing was conducted over 2 years at a single commercial game rearer in Worcestershire. In 2016, we reared 3000 Control and 3000 Enhanced pheasants in 4 runs of 800 birds (large runs) and 8 runs of 350 birds (small runs). In 2017, we reared 1750 Control and 1750 Enhanced pheasants in 2 runs of 800 and 6 pens of 350. The number of birds (both Enhanced and Control) that were released were 5700 in Year 1 and 3200 in Year 2.

Pheasants were reared for the first two weeks in night-sheds (2.5 x 2.5m for small night-sheds, 3.6m x 3.6m for large night-sheds) before being given access to larger fenced and netted exterior runs which constituted 70m^2 for small runs and 170m^2 for large runs. Pheasants were reared until 6-7 weeks old before release. For Control birds, the runs were flat, effectively two-dimensional areas with feeders and drinkers as their only additional features. The diet for Control birds consisted entirely of the Bartholomews pheasant feed range, starting with Chick Crumb from day old chick to two weeks old, then Chick Micro from two weeks old to four weeks old, then Grower Mini pellets until release. For Enhanced birds, we added to the Control diet live mealworms (from Live Foods Direct) that comprised 1% by weight of the Control diet and mixed seed (Ruddings Wood Wild Bird Seed Blend) that comprised 5% by weight of the Control diet. Dietary enhancements would be supplied to the Enhanced birds each morning and were scattered over a wide area of the pens to deter any individual pheasant from monopolising the feed. The quantities of both seed and mealworm per birds were recalculated on a weekly basis alongside the weekly increases in standard feed to ensure that increases were consistent (Table 2.1).

Pheasant age in weeks	1	2	3	4	5	6	7
Chick feed per bird per day (grams)	10	21	27	38	42	46	50

Table 2. 1 Feed budget by weight of pheasant chicks during rearing.

Enhanced birds were also provided with perching material from day 1. To make the process of constructing perches as easy and cost effective as possible, perches in 2016 were constructed from a scaffold of either delivery pallets (1mx1m) or disused metal fencing (1.5mx1m) (Fig 2.1). Upon these scaffolds were attached a selection of coppiced hazel branches to provide as natural a perching surface as was possible. This resulted in ~5m of perching material for the smaller perches and ~10m for the larger metal-based perches from a range of different hazel diameters to try and best simulate real perching material found in trees and shrubby cover. A single small (1mx1m) perch was placed within both the small and large night-sheds due to size restrictions. Once the pheasants were allowed access into the exterior runs at 2 weeks of age, the small runs were provided with an additional ~10m of perching material while the large runs were provided with an additional ~30m of perching material, resulting in ~0.042m of perching per bird in the small runs and ~0.043m per bird for the large runs. In 2017, the perch design was altered to be more space efficient, producing 3 new designs. Large perches were freestanding A-frames that had 7x3m batons as perching (Fig 2.1), large night-shed perching ladders had 5x1.5m perching, and small night-shed ladders had 5x1m perching. Small runs of 350 birds had 1 large perch on the exterior and one small night-shed ladder within the nigh-shed interior, resulting in 0.074m of perching per bird. Large runs of 800 birds had 2 large perches on the exterior and 2 large night-shed ladders on the night-shed interior, resulting in 0.071m of perching material per bird. The amount of perching provided was primarily determined by the amount of space the game rearer was willing to allow. Although Whiteside, Sage, and Madden (2016) used 0.21m per bird, one of the main objectives of our study was to see if these methods can be transferred from small, specifically designed rearing environments into those of a commercial setting, and as such we were forced to work within the confines prescribed by the game rearers. Additionally, although the allotted space per perch appears small, that is the minimum amount of perching available to a bird if all were to perch at the same time. In reality, this is extremely unlikely to happen, and if a more realistic 20% of the birds within the run are using the perches at any one time, each bird could access around 0.21m in 2016 and 0.35m in 2017 of perch space.

Figure 2. 1 A) Large perches based on a metal frame using coppiced hazel used in Year 1; B) Small perches based on wooden pallet frame used in Year 1; C) Large perches based on a wooden A-frame used in Year 2.

Pheasants were released between 6-7 weeks of age onto six shoots in 2016 and four in 2017, with two of 2017's being used in the previous year and two new. In 2016, we released equal numbers of Control and Enhanced birds into each of 18 pens, and in 2017 we released equal numbers of Control and Enhanced birds into 11 pens (Table 2.2). We marked each bird according to its release pen and rearing condition using coloured patagial tags (Roxan Livestock Identification, Selkirk). Light-weight Multi-Tags were used in Year 1, but these were replaced with the more durable Plastags in Year 2. Most shoots released approximately equal numbers of male and female pheasants. However, Site 3 released only males as part of their overall pheasant release management strategy. All sites were lowland farmland shoots releasing into either coniferous, deciduous, or mixed woodlands. All shoots practiced some degree of game cover planting and all release pens and release practices broadly conformed to the description given in the introduction of this thesis. Various levels of gamekeeping were carried out by the differing shoots, with the shoot Size classification described further in this chapter accounting for broad differences in gamekeeping effort.

	OS Grid Reference	Released Tagged Birds Relative to Total Number of Pheasants Release Over the Entire Shoot Year 1	Released Tagged Birds Relative to Total Number of Pheasants Release Over the Entire Shoot Year 2	Pens Year 1	Pens Year 2
Shoot 1	SO 64303 71069	2000/10000	-	5	0
Shoot 2	SO 63234 64496	400/400	-	3	0
Shoot 3	SK 79126 02398	1000/2500	1600/2500	1	2
Shoot 4	SO 62837 58424	800/800	800/800	2	2
Shoot 5	SO 60997 65720	700/700	-	4	0
Shoot 6	SO 60048 71171	-	500/500	0	4
Shoot 7	SO 55996 63677	800/800	-	3	0
Shoot 8	SO 59022 64313	-	600/600	0	3

Table 2. 2 Broad locations, release numbers, and pen numbers of the participating shoots over the two years of the project.

2.2.2 Tag Returns

Shot pheasants were checked for tags at the end of each shoot day over the course of the shooting season (Oct 1st-Feb 1st), with rearing Treatment, year of release, and pen of release identified by tag colour. Any previous year's tags that were collected in Year 2 were also recorded to compare year-to-year survival. Records of Year 2 tags were also provided from two shoots in 2018. The pens were also categorised based on the total number of birds (both tagged and non-tagged) released upon that entire shoot. These categories were Small, Medium, or Large shoots with releases of 0-600, 601-2000, and >2000 respectively. Categories were chosen, as opposed to using release size as a continuous variable, because these three categorisations also broadly represent the gamekeeping effort carried out on each of the shoots, with Small carrying out very limited gamekeeping, Medium carrying out non-intensive keeping efforts, and Large having employed profession gamekeepers on a regular or fulltime basis. Gamekeeping effort broadly covers aspects such as how often feeders are refilled, predator control, release pen maintenance, etc, with increased gamekeeping effort representing better quality pheasant management and likely leading to increased harvest rates. As such, subdividing the pens into these three categories may highlight differing harvest rates between Enhanced and Control pheasants in relation to the quantity of pheasant management that the shoot carries out.

Additional variables that were collected regarding each shoot and used during the analysis are show in Table 2.3.

Variable	Definition
Tag Returns	The numbers of recorded tags from shot pheasants over the entire shooting season from each pen separated by Treatment.
Treatment	Whether the pheasant was reared under Enhanced or Control conditions.
Stocking Density	Pen stocking density in m^2 of release pen area per bird, calculated by using a handheld GPS to measures the size of the release pen and dividing it by the number of pheasants released within that pen.
Release to Season	The number of days between pheasant release and the legal start of the shooting season (Oct 1st).
Release Size	Combined total of tagged and untagged pheasants released on the shoot: Small (<600), Medium (601-2000), and Large (>2000).
Year	Year of the study (Year 1 or Year 2).
Pen ID	The name of the pen.
Shoot ID	The name of the shoot where the pens were located.

Table 2. 3 Definitions of the variable abbreviations used in the statistical analysis

2.2.3 Statistical analysis for harvest rates

All statistical analysis was carried out in R version 3.6.1 (R Core Team, 2018) using the lme4 (Bates *et al.*, 2015), mgcv (Wood, 2011), gam (Wood, 2017), and MuMin (Barton, 2019) packages.

The primary question that this investigation sought to answer was whether there was a difference between the rates at which Enhanced and Control pheasants were harvested. To answer this, three Generalised Linear Mixed Effect Models were used with the absolute Tag Returns as the dependant variable. As Tags were count data, a poisson model family was used. These models included Pen IDs and Shoot IDs as random effects. This allowed Enhanced and Control birds from the same pens to be modelled against each other directly and accounted for differences between release pens that were not used as independent variables, such as the total number of birds released into the pens which ranged from 50-1000. Pen ID was then nested within Shoot ID, accounting for additional differences between shoots that were not used as independent variable within the models, such as management practices.

A series of model structures were adopted to investigate the results. As the number of pens was relatively low (n29) and the number of independent variables, some of which may correlate, was high, a smaller model containing only Treatment as an independent variable was first created to investigate the central question of ‘does rearing treatment affect harvest rates’. This model is referred to as Treatment GLMM. After this, a larger model was created to investigate the other factors that might impact on the harvest rates of Treatment. The independent variables that were added to this model were Treatment, Stocking Density, Year, Release to Season, Release Size, and their two-way interactions. Three-way interactions were not included as their addition would decrease the statistical power of the model to a high degree due to its small sample size. However, there was high collinearity between Release Size and release dates (Release to Season), with Large shoots releasing earliest, Medium shoots releasing latest, and Small shoots releasing between the two. To avoid the effects of collinearity within the models, the larger model was separated into two models; one that removed Release Size (DATE GLMM) and one that removed Release to Season (SIZE GLMM). I then applied the Dredge function to both models. This function generates a selection table of models comprising of combinations (subsets) of the fixed effect terms from the original model that Dredge was applied to, providing an AIC value for each model subset which can then be compared to identify which combination of the fixed effects produces a model with the lowest AIC. This is often superior to methods such as stepwise regression as fixed effects that have been removed at one stage in stepwise may in fact improve model AIC in successive stages after additional fixed effects have been removed. The model with the lowest AIC was selected as the criteria to select the best model as reducing model AIC is considered an appropriate method of improving model accuracy (Akaike, 1974). However, when using the dredge function to select the best model the user must bear in mind that it is possible for the dredge function to produce models that have the lowest AIC but whose variable combinations make little realistic sense, so caution must always be taken to assess the practical viability of the ‘best’ model selected by the Dredge function. When selecting between models via the lowest AIC value, those model structures with an AIC difference of <2 can also be considered to have equally substantial support(Burnham and Anderson, 2004), in which case the additional reasons for selecting one model over the other should be explained.

After running the Dredge function, Year, Density, and all their interactions were removed from both DATE GLMM and SIZE GLMM as they had no statistically significant effects and retaining them increased model AIC by >2. An error arose on the DATE GLMM with near non-convergence due to a very high eigenvalue, with the model output suggesting that rescaling one of the variables may solve this issue. As such, Release to Season was square-rooted, resulting in the desired elimination of non-convergence. When these results are presented graphically (Figure 2.2) the graph is based off of Date GLMM without square-rooting Release to Season to enable easier visual interpretation.

When SIZE GLMM was run, the model produced a singular boundary fit warning. This is caused by some dimension of the variance-covariance matrix having been estimated as exactly zero. The likely cause of the singularity is from the model overfitting from data that has poor statistical power, likely from the small sample size. There is not yet a consensus on how to deal with such singularity errors. As this model has been reduced down to its most simple form by the Dredge package (independent variables being: Treatment, Release Size, and their interaction), removing any of the remaining variables to remove the singularity, as suggested by Barr et al (2014), would render the model useless for the question it sought to answer. As such, the most effective method of retaining the model’s purpose but also removing the singularity error was to remove Shoot ID from the random effect, leaving just Pen Name. Once removed, the results of the Size GLMM differed very little from when Shoot ID was included; however it must be noted that some of the descriptive power of this model had been lost. All three final GLMM structures can be seen in Table 2.4.

Model Name	Dependant Variable	Independent Variables	Random Effect
Treatment GLMM	Tag Return	Treatment Type	Shoot ID /Pen ID
DATE GLMM	Tag Return	Treatment Type	Shoot ID/Pen ID
		Square rooted Release to Season	
		Interaction between Treatment and Sqrt(Release to season)	
SIZE GLMM	Tag Return	Treatment Type	Pen ID
		Release Size	
		Interaction between Treatment and Release Size	

Table 2. 4 Final GLMM models structures use for Tag Return analysis.

2.2.4 Collecting biometrics data

I investigated the effects of Treatment on pheasant morphology by collecting and analysing biometric data from birds that had been shot in an effort to identify the biological effects of Enhanced Rearing and to identify any effects that may have directly impacted pheasant survival post-release. In the last 2 shoot-days of the Year 1 season at Site 3, I collected a total of 28 male pheasants for dissection. In Year 2, 12 male birds were collected from Site 3 from each of the first 8 shoot-days with the exception of one day where only 8 males were collected. An additional 39 were collected on the last shoot-day, totalling 133 carcasses. Additionally, the weights of shot, tagged, male pheasants were also taken on shoot-days at Site 3 over both years using a spring-balance to an accuracy of 5g. When combined with the dissected carcasses, this provided weights for 135 pheasants from Year 1 and 385 from Year 2.

Each of the 133 collected carcasses were dissected after being weighed (AMIR Digital Kitchen Scale, precision 1.0g) and having Tarsus length (Year 1 only) and tarsus diameter measured (Tacklife DC01 digital calipers, precision 0.1mm). During dissections, both pectororalis and supracoracoideus muscles were removed and weighed together to form the Breast Muscle measure (Triton T3 scales, precision 0.01g). The heart was also removed and weighed, and so was total body fat in Year 1 and cloacal fat in Year 2. These organs and tissues were chosen as they may have some direct effect on pheasant survival and help further explain how Enhanced Rearing may have affected harvest rates. Breast muscle weight was taken as it could be easily removed in a consistent manner and could stand as a proxy for the pheasant's total body muscle mass. Heart weight was taken as a measure of cardiovascular strength, directly impacting a pheasant's ability to fly and overall fitness. Fat weight was taken as a measure of energy reserves during winter, with fatter pheasants having foraged more effectively and needing to do so less in the future, reducing opportunities for predation. In Year 2, cloacal fat alone was taken as the fat measure as it has been shown to be an effective proxy for total body fat (Draycott *et al.*, 2002) and is much easier to remove in its entirety. These three organs and tissues had not been studied before in either of the perch provisioning studies or the diet improvement study (Whiteside, Sage and Madden, 2015, 2016; Santilli and Bagliacca, 2017). Biometrics values were then standardised to be relative to overall body weight by dividing each biometric's weights (g) or lengths (mm) by the total body weight of the pheasant (g). Descriptions of each biometric variable and all other variables used in the biometric analysis can be found in table 2.5.

Variables	Definition
Weight	Total body weight of the pheasant to the nearest 5g for pheasants weighed with spring balance and 1g for those weighed during dissections.
% Breast Muscle	Both pectororalis and supracoracoideus muscles were removed from both breasts and weighed to the nearest 0.01g. Their weight was then converted to a percentage of total body weight.
% Heart	Heart was removed, emptied of blood, and weighed to the nearest 0.01g. Its weight was then converted to a percentage of total body weight.
% Total Fat	Year 1 only. As much of the body fat as could be feasibly removed was taken from the entire carcass and weight to the nearest 0.01g. Its weight was then converted to a percentage of total body weight.
% Cloacal Fat	Year 2 only. Cloacal fat was removed in its entirety and weighed to the nearest 0.01g. Its weight was then converted to a percentage of total body weight.
Tarsus Diameter Ratio	Diameter of tarsus above the spur was measured to the nearest 0.1mm using digital callipers. This length was then divided by the total body weight.
Tarsus Length Ratio	Year 1 only. Length of the tarsus was measured to the nearest 0.1mm using digital callipers. This length was then divided by the total body weight.
Treatment	Whether the bird was reared under Enhanced or Control conditions.
Days Since Release	The number of days between release and the date the pheasant was shot.
Year	The year of the project (Year 1 or Year 2)

Table 2. 5 Definitions of variables used in Biometric analysis

2.2.5 Statistical analysis for biometric data

I tested whether rearing Treatment affected weight, tarsi, breast muscle, heart, and fat by conducting a GLM and a GAM for each biometric measure. Days Since Release was included as an independent variable to account for growth over time and Year was included to account for the increased perching material provided to the pheasants in Year 2 and any environmental or management differences that occurred between years. GAMS were used, with Days Since Release as a smoothing independent variable for polynomial regression between Days Since Release and the dependent variable. These GAMs were compared to GLMs as they could potentially account for non-linear relationships in biometrics over time whereas GLMs only account for linear relationships. This is of particular note as biometrics were all standardised using total body weight, and disparities in weight gain might arise between continued growth of juvenile pheasants and the onset of winter reducing body fat.

The Dredge package was then used to remove independent variables and/or interactions that increased model AIC until the model with the lowest AIC remained, both for GLMs and GAMs. If the final reduced model for any of the biometrics removed Treatment as an independent variable, indicating that Treatment had no statistically significant effect on that specific biometric, the results are not presented graphically, and model structures were not included in Table 2.6. Whichever model had the lowest AIC for each biometric, either the GLM or GAM, was used for the analysis. The final minimal model structures containing Treatment with the lowest AIC for each biometric are shown in Table 2.6.

2.2.6 Ethical Concerns

To clarify the project regarding ethics, all alterations to the rearing process were done to improve pheasant fitness and welfare and were overseen by professional pheasant rearers within their much broader commercial gamebird rearing operations. Some limited tagging had been carried out previously by the rearers, and the tagging for this project integrated within their own practices. Once released to the shoots, all pheasants were managed to the discretion of their respective shoot owners in accordance with their own practices with no additional steps taken as a result of this project other than the counting of tags at the end of shoot-days. No pheasant were shot or killed specifically for this project. Instead, they were shot as a part of each shoot's standard release and shooting regime, all within the legal shooting season for pheasants. All dissected pheasants were provided freely by Site 3 on the day they were shot. Aside from the initial rearing enhancements, designed to improve welfare and fitness within the rearing environment, and the tagging, live pheasants were not directly interacted with in any way by this project.

Model Name	Dependant Variable	Independent Variables
Weight GLM	Weight	Treatment
		Days Since Release
		Year
		Interaction: Treatment, Day since Release
Breast Muscle GAM	% Breast Muscle	Treatment
		Year
		Interaction: Treatment, Year
		Smoothed Variable: Days Since Release
Heart GAM	% Heart	Treatment
		Smoothed Variable: Days Since Release
Tarsus Diameter GAM	Tarsus Diameter Ratio	Treatment
		Year
		Interaction: Treatment, Year
		Smoothed Variable : Days Since Release

Table 2. 6 Final GLM and GAM model structures used for Biometric analysis where Treatment was a significant variable

2.2 Results

2.3.1 Tag Returns

2.3.1.1 Did rearing treatment alone result in significantly different Tag Returns – Treatment GLMM

Rearing Treatment had a statistically significant effect on the numbers of recorded Tag Returns, with Enhanced Tag Returns being ~10% higher than Control Tag Returns overall (Estimate = 0.101, Std Error = 0.0433, P = 0.0198).

2.3.1.2 Did release date (Release to Season) affect the relationship between Tag Returns and Treatment? – DATE GLMM

Enhanced Tag Returns were predicted as being recorded at a lower rate than Control Tag Returns when days between release and the start of the shooting season were 0 (Estimate = -1.14, Std Error = 0.499, P = 0.022, Fig 2.2). Enhanced Tag Returns then increasing at a higher rate than Control Tag Returns by 1.44% for every increase in days between release and the start of the shooting season (1st October) (Estimate = 0.183, Std Error= 0.0731, P = 0.0124, Fig 2.2). Our model predicted the mean per-pen harvest sizes of Enhanced birds surpassing Control harvests on releases that occurred 40 days (August 22nd) prior to the legal start of the shooting season. Year (Estimate = -0.078, P = 0.385) and Stocking Density (Estimate = -0.005, P = 0.743) did not significantly affect the relationship between Enhanced and Control Tag Returns in this model.

2.3.1.3 Did Release Size affect the relationship between Tag Returns and Treatment? – SIZE GLMM

On Large shoots, mean Enhanced Tag Returns were predicted as being +17.4% (±32.8%) higher than Control Tag Returns (Estimate = 0.160, Std Error = 0.0548, P= 0.003, Fig 2.3, Table 2.7). This rate did not differ significantly on Small shoots (Estimate = -0.01, Std Error = 0.143, P = 0.942), where the model predicted mean Enhanced Tag Returns as being recorded at a +16.2% (± 31.0%) higher rate than Control Tag Returns. However, on Medium shoots, mean Enhanced Tag Returns were predicted as being -6.296% (±30.371%) lower than Control Tag Returns (Estimate = -0.221, Std Error = 0.101, P = 0.028). Year (Estimate = -0.134, P = 0.151) and Stocking Density (Estimate = -0.027, P = 0.176) did not significantly affect the relationship between Enhanced and Control Tag Returns in this model.

Release Size		Control	Enhanced	Number of Pens
Large	Mean Tag Returns per pen Std Error	62.1 20.4	72.9 23.9	8
Medium	Mean Tag Returns per pen Std Error	13.8 4.2	13 3.96	11
Small	Mean Tag Returns per pen Std Error	7.8 2.43	9.06 2.81	10

Table 2. 7 Mean predictions of numbers of Tag Returns per release pen between the different release sizes classifications.

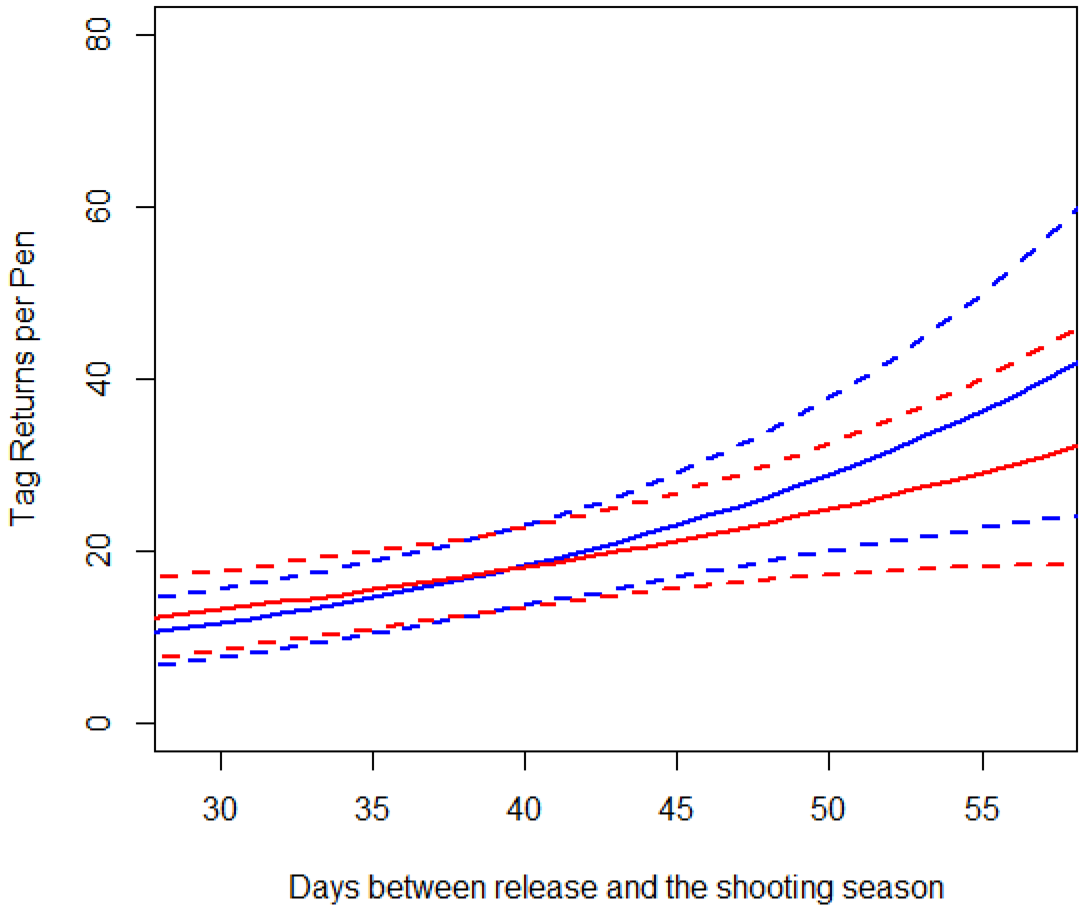

Figure 2.2 Predicted change in the per pen mean Enhanced (Blue) and per pen mean Control (Red) Tag Returns across different release dates as shown by their proximity to the start of the shooting season. X axis values not square-rooted (as they were in the model) to enable easier visual interpretation.

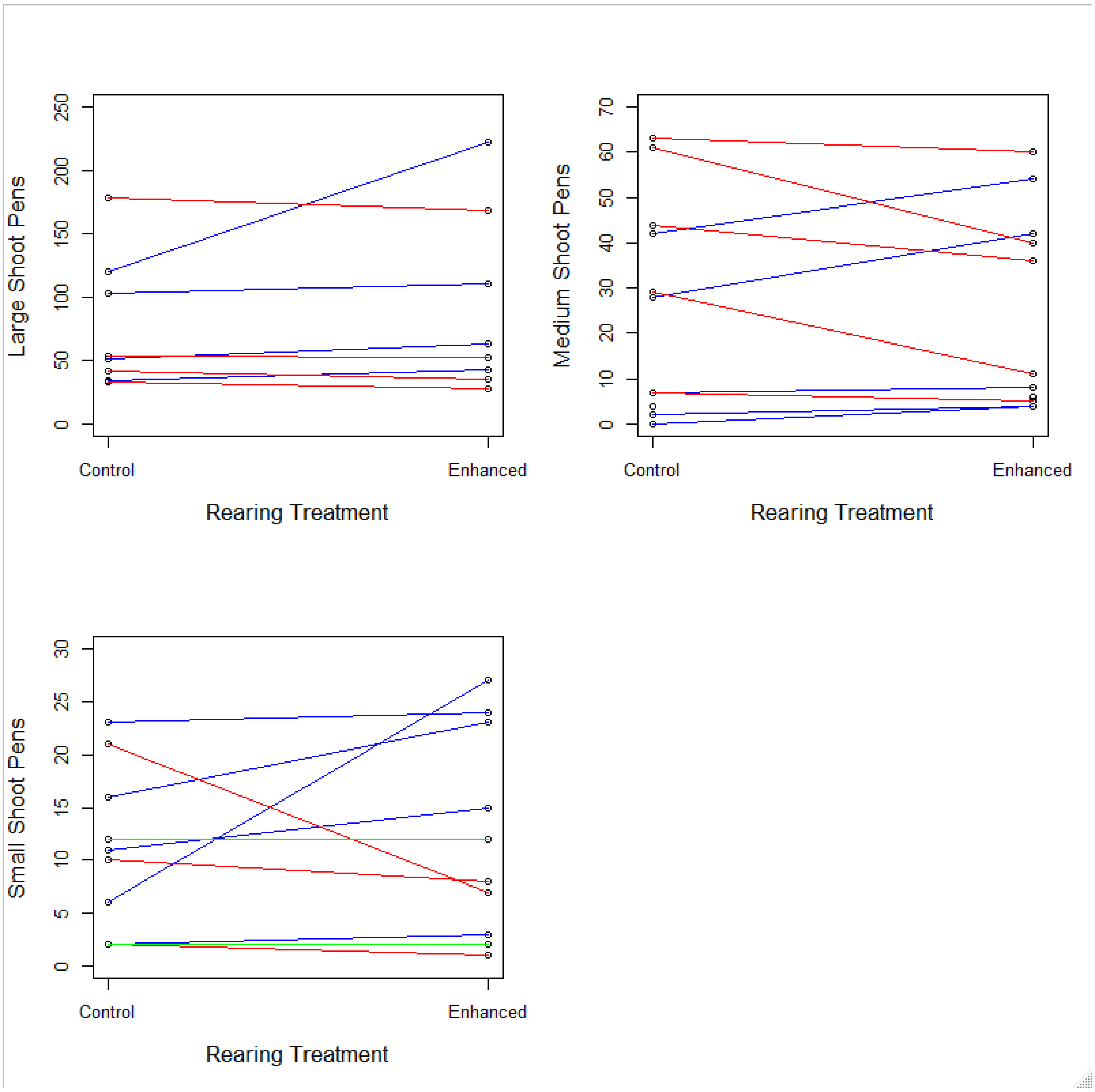

Figure 2. 3 Graphs showing Tag Returns (y axis) for each of the Treatment types (x axis) from each pen separated by shoot size classification (Large, Medium, Small). For each pen, Blue lines indicate higher Enhanced Tag Returns, Red lines indicate higher Control Tag Returns, and Green lines indicate no statistically significant difference in Tag Returns between Treatments.

2.3.1.4 Year to Year survival

Two shoots in the 2017/2018 shooting season and 2 shoots in the 2018/2019 shooting season recorded tags from previous years in their game bags, reporting a total of 16 tags of the 4400 tagged pheasants released. The numbers were too low for any meaningful statistical comparison, but overall three times more Enhanced tags from previous years were recovered than Control tags (Table 2.8).

Year of Release	Season Recovered	Enhanced Tags	Control Tags	Number Released
2016	2017-2018	2	0	800
2016	2017-2018	4	1	1000
2017	2018-2019	4	2	1800
2017	2018-2019	2	1	800
Total		12	4	4400

Table 2. 8 Second year tags collected from four release shoots across two years.

2.3.2 Biometric analysis

2.3.2.1 Body Weight – Weight GLM

Enhanced and Control pheasants did not differ in body mass on the day of release (Estimate = 42.3, P = 0.377), but Enhanced pheasants then gained weight more slowly post-release such that they were lighter for their age when shot (Estimate = -0.8, P = 0.023, Fig 2.5). The model predicted that Enhanced birds gained 1.37g/day after release whereas Control birds gained 2.19g/day after release. Overall, birds in 2017 were lighter than those in 2016 (Estimate = -0.816, P = 0.023).

2.3.2.2 Breast Muscle - %BM GAM

In Year 1, Enhanced Pheasants' percentage breast muscle weight was higher than that of Control Pheasants' (Estimate = 1.1807, P = 0.044, Fig 2.6). The model predicted that this resulted in a +7.306% (± 2.617%) increase in Enhanced percentage breast muscle weight by the final day of shooting (day 175). In Year 2, pheasants percentage breast muscle weight was higher than Year 1 for both Control and Enhanced pheasants (Estimate = 2.591, P= <0.001 Fig. 2.6), but Enhanced pheasants' percentage breast muscle weight was no longer significantly different to Control pheasants' (P = 0.285). The effect of days since release did not differ significantly between Treatments as an independent variable in the GLM (P = 0.552) or as a smoothed independent variable in the GAM (Enhanced: P = 0.769. Control: P = 0.999). It is worth noting that Enhanced pheasants were harvested at a higher rate than Control in Year 1 at the site where dissected birds were collected but were not harvested at a higher rate than Control at that site in Year 2. This may mean that there is a relationship between larger Breast Muscle size and increased harvests.

2.3.2.3 Heart - % Heart GAM

Enhanced pheasants had higher percentage heart weight than Control (Estimate = 0.025, P = 0.001, Fig 2.7). The model predicted that this resulted in a +4.461% (± 1.672%) increase in Enhanced percentage heart weight by the final day of shooting (day 175). The effect of days since release did not differ significantly between treatments as an independent variable in the GLM (P = 0.660) or as a smoothed independent variable in the GAM (Enhanced: P = 0.686. Control: P = 0.998). Year also did not significantly affect percentage heart weight between Treatments (P = 0.426).

2.3.2.4 Tarsus Diameter - Tarsus Diameter GAM

In Year 1, Enhanced pheasants had larger Tarsus Diameter Ratios than Control (Estimate = 0.0004, P = 0.036, Fig 2.8), meaning that they had larger tarsi relative to body weight. The model predicted that this resulted in a +6.2% (± 2.82%) increase in Enhanced tarsi diameter by the final day of shooting (day 175). In Year 2, both Control and Enhanced percentage tarsus diameters ratios increased (Estimate = 0.00036, P=0.03, Fig 2.7), but Enhanced percentage tarsus diameter ratios were no longer significantly greater than Control (P = 0.765). The effect of days since release did not differ between Treatments (P = 0.362). Again, it is worth noting that Enhanced pheasants were harvested at a higher rate than Control in Year 1 at the site where dissected birds were collected but were not harvested at a higher rate than Control at that site in Year 2. This may mean that there is a relationship between larger tarsus diameters and increased harvests.

2.3.2.5 Cloacal Fat (Year 2 only) - % CF GLM

Enhanced pheasants' percentage cloacal fat did not differ statistically from Control (Estimate = -0.205, P = 0.628), but overall percentage cloacal fat did increase with increased Days Since Release (Estimate 0.01, P = <0.001).

2.3.2.6 Total Body Fat (Year 1 only) - % TBF GLM

Enhanced pheasants' percentage total body fat did not differ significantly from Control (Estimate = 0.835, P = 0.976), nor did it change significantly with increased Days Since Release (Estimate = 0.115, P = 0.424).

2.3.2.7 Tarsus Length (Year 1 only) - % TL GLM

Tarsus Length Ratio did not differ significantly between Treatments (Estimate = 0.004, P = 0.117. Nor did it differ significantly with increased Days Since Release (Estimate -1.911e-05, P = 0.919).

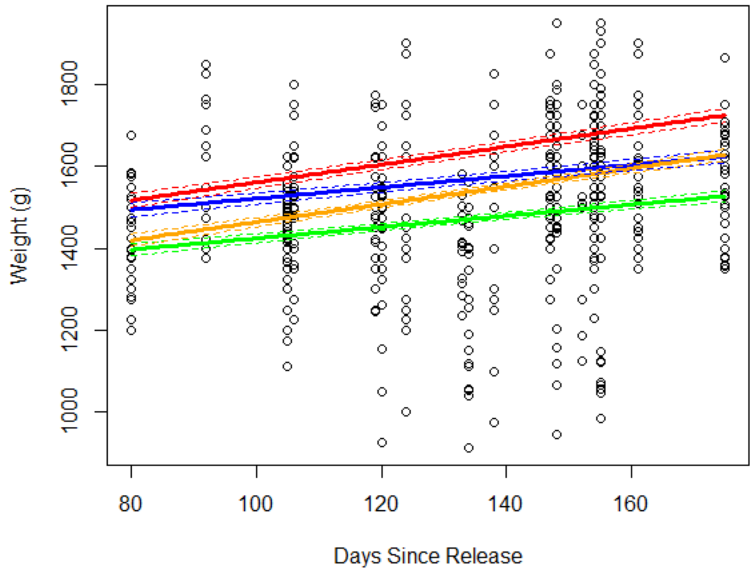

Figure 2. 4 Predicted mean weight gain in Enhanced and Control pheasants over time across Years 1 and 2 (Control Year 1 = Red, Control Year 2 = Orange, Enhanced Year 1 = Blue, Enhanced Year 2 = Green).

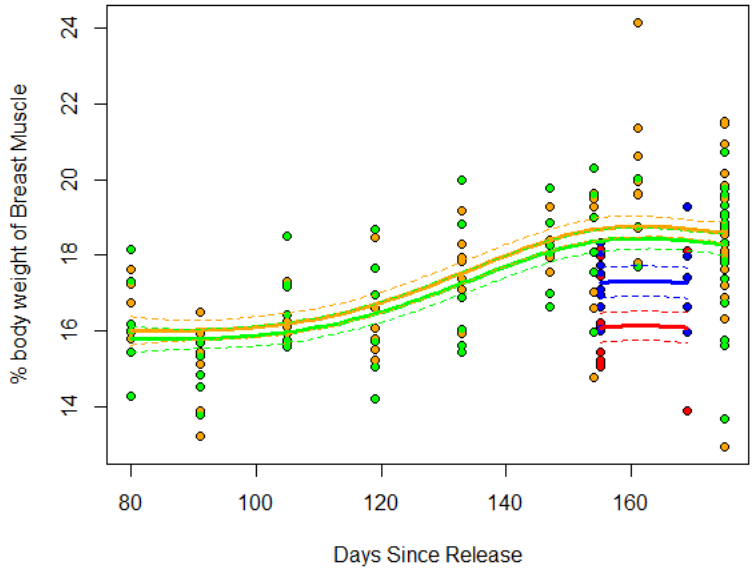

Figure 2. 5 Predicted mean breast muscle weight as a percentage of total body weight between Treatments and Year (Control Year 1 = Red, Control Year 2 = Orange, Enhanced Year 1 = Blue, Enhanced Year 2 = Green) over days since the pheasants were released.

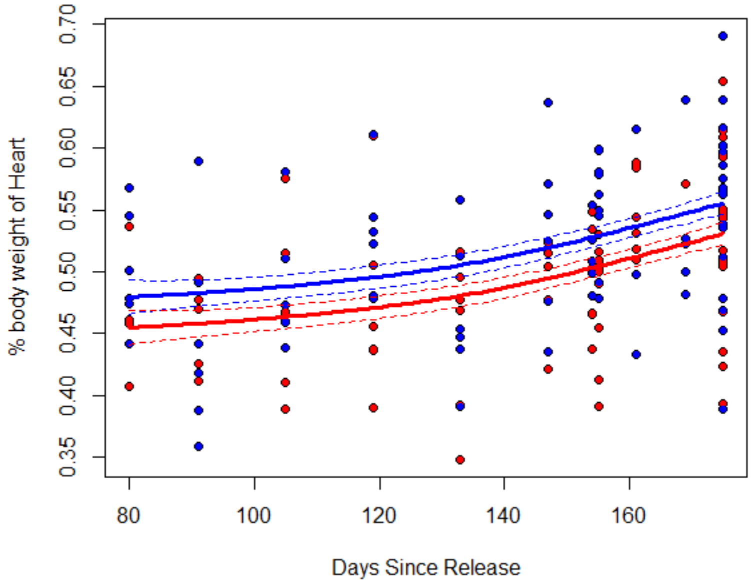

Figure 2. 6 Predicted mean heart weight as a percentage of total body weight between Treatments (Control = Red, Enhanced = Blue) over days since the pheasants were released.

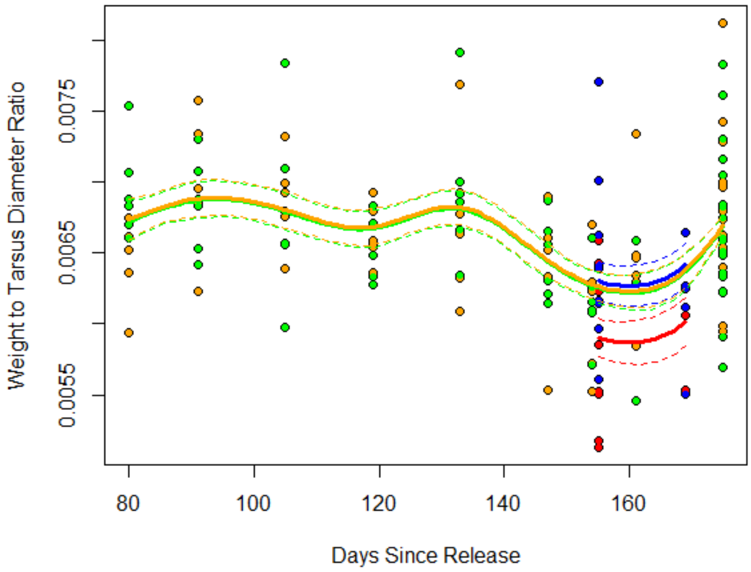

Figure 2. 7 Predicted mean Tarsus Diameter Ratio between Treatments and across Years 1 and 2 (Control Year 1 = Red, Control Year 2 = Orange, Enhanced Year 1 = Blue, Enhanced Year 2 = Green) over days since the pheasants were released.

2.4 Discussion

By combining both a more natural diet and the provisioning of perching material, we show that deploying the Enhanced Rearing methodology within a commercial pheasant rearing environment can lead to greater pheasant harvests. However, although this could bring increases in harvest of 16-17%, such benefits were not encountered across all shoots, but instead only became apparent on shoots that released birds earlier. Our model predicted that for a pen that harvested the mean quantities of Enhanced and Control birds, Enhanced birds harvests would surpass Control for pens that released at least 40 days before the legal start of the shooting season. They were also only shot at a higher rate in my sample in pens on Small and Large shoots and not on the Medium sized shoots. Birds reared under enhanced conditions gained weight at a rate of 0.82g/day less than Control birds post-release. This effect was consistent between years. Enhanced pheasants were also shown to have consistently larger hearts between years but only larger breast muscles and tarsus diameters in the year when they were shot at a higher rate than Control on the site where dissected birds were collected.

The provisioning of perching material likely enabled pheasants to develop roosting behaviours that fostered a greater tendency to spend time off the ground following release (Whiteside, Sage and Madden, 2016). This would limit their exposure to terrestrial predators, specifically the red fox which is their primary predator (Sage *et al.*, 2018), and in doing so increase harvest rates because more birds survive to the point of harvest. The greatest effect may have come from increased roosting at night, when foxes are most active and pheasants most vulnerable, and the provisioning of perches has been shown to increase nocturnal roosting in captive-reared chickens (Olsson and Keeling, 2000). Beyond the benefits brought from increased roosting, the provisioning of perching material has also been shown to increase spatial working memory in both pheasants (Whiteside, Sage and Madden, 2016) and chickens (Gunnarsson, Yngvesson and Keeling, 2000). This in turn could have positive impacts on navigation in the wild (Cristol *et al.*, 2003), foraging efficiency (Garber, 1990), and more efficient habitat use (Howery, Bailey and Laca, 1999), all of which would improve pheasant survival to harvest.

The Enhanced Rearing process also involved increasing dietary variety. A more natural early life diet increased vigilance behaviours and reduced foraging times post-release (Whiteside, Sage and Madden, 2015), both of which further reduce the risk of predation by decreasing exposure times and increasing the likelihood of identifying and subsequently evading a predator (Lima, 1987; Guillemain *et al.*, 2007). However, the same dietary improvements as I carried out did not increase the number of pheasants harvested in the year of release in Whiteside, Sage, and Madden’s (2015) study, but rather only increased year-to-year survival. Although there was an indication that this occurred in my study (from >1 year tag returns), my dietary enhancements may have also increased immediate pheasant harvests through reinforcing benefits brought about by enriching their environment with perches. Combining dietary and environmental enrichment has been shown previously to have positive effects on improving natural foraging behaviours in captive reared animals beyond what dietary improvements can do alone (Brown, Davidson and Laland, 2003), and combining both may have further increased any benefits to the pheasant’s neural plasticity that were brought about by a single one of the enrichments alone (Gro *et al.*, 2013). This would be of particular importance to pheasants post-release, as they are placed into an entirely novel environment where their very survival depends on the development of skills that they have had no previous experience with, namely predator avoidance.

I detected no effect of stocking density on either overall harvest rates or differential harvest of Enhanced or Control birds. This is surprising because previous studies have shown that increased stocking densities reduced harvest rates (Turner, 2007). A possible explanation for this null result is that most of my study sites practiced high stocking density. Half of my study pens released pheasants with less than 5m^2 of pen area per bird and only 1 operated a density lower than the 700 birds per hectare GWCT recommendation (Sage and Swan, 2003). However, a more recent meta-analysis of shooting across the entire UK found no evidence of release density negatively affecting harvest rates (Robertson *et al.*, 2017).

Shoots that released their birds earlier in the year reported larger Enhanced harvests. We suspect that this occurred because the longer the birds were in the wild, the greater their exposure to predation and thus the longer the advantages gained by Enhanced Rearing would have to contribute to survival, increasing their relative harvest rates. This does not explain why Control pheasants were harvested at a higher rate on late releases though, but this result may also explain the different harvest rates from release sizes, with the broad release times in my study being Large and Small shoots releasing earlier and the Medium shoots releasing later. An additional explanation for this difference between release sizes is dispersal. Shoots investing in larger releases also invest in significant habitat management to support and maintain those additional birds, while most habitat management on the Small and Medium shoots in my study was via providing strips of game cover alone. Pheasant home ranges are smaller when more ideal habitat is present (Leif, 2005), and increasing pheasant roosting behaviours may have made the birds more selective in their habitat choice, leading to greater dispersal if ideal habitat was in shorter supply. This may have negatively affected Medium shoots but not Small as the limited amount of high-quality habitat that occurs naturally within the landscape could have been sufficient to support Small shoots' lower releases sizes. However, both Whiteside, Sage, and Madden's improved diet study (2015) and provisioning of perching material study (2016) examined dispersal and found that it was not affected by improving rearing condition. Although, it is worth noting that these studies were both carried out on what would be classified as a Large shoot in my study, potentially reducing dispersal as theories above. A study of Enhanced pheasant dispersal would be required to definitively assess this theory.

Several of the morphological differences between Treatments on the carcasses collected from Site 3, namely increased tarsus diameter and breast muscle, were present in Year 1 but not Year 2. Likewise at Site 3, Enhanced pheasants were harvested at much higher rates than Control in Year 1 but not Year 2, implying that these morphological changes are indicative of higher harvest levels. Increased movement to and from roosts in trees and shrubby cover would have strengthened breast muscles (Butler, 1991). Likewise, the thickening of the tarsus would have occurred from spending greater time gripping onto rearing perches and then branches instead of simply sitting on the ground (Enneking *et al.*, 2012;

Whiteside, Sage and Madden, 2016). However, increased breast muscles may have further improved Enhanced harvests by increasing wing-assisted incline running (WAIR). WAIR is the primary method of immediate predator escape used by Galliformes (Dial, 1990), whereby strong bursts from the wings are used to give an immediate boost to running speeds to escape predation. This would have increased Enhanced bird fitness even further, feeding into their advantage from lowered predation levels and earlier releases. Also, WAIR's bursts of muscle activity are more reliant on immediate muscle strength than circulatory capacity (Butler, 1991; Nespolo *et al.*, 2018), and this might explain why despite Enhanced pheasants having larger hearts in both years, harvest rates were only higher in the year when breast muscles were larger.

The same rates of reduced weight gain over time post-release in Enhanced birds were also present in both years, implying that it too did not affect harvest rates. This is despite wild pheasants also weighing less than pen-reared birds but having far higher survival rates (Musil & Connelly, 2009; Robertson et al, 1993). The model also predicted that on the actual day of release, Control birds were not significantly heavier than Enhanced. However, this result in of itself is in direct contrast to both Whiteside, Sage, and Madden (2016) and Santilli and Bagliacca (2017), who found that pheasant reared with perching material were heavier on release. This alludes to there being another mechanism present in the combination of both diet and perching material causing reduced weight gain. This reduction in weight of Enhanced pheasants might prove detrimental to the game meat industry.

At Site 3, the increased harvest of Enhanced birds was only evident in Year 1 (2016), as were the effects of larger breast muscles and thicker tarsi. This implies that for Enhanced Rearing to be effective, these two morphological traits must also be present. Figure 2.6 and 2.8 appear to show that the breast muscle and tarsi of Site 3's Control birds in 2017 were more similar to those of Enhanced birds as opposed to Enhanced birds never developing those morphologies, which may have caused the similarity in their harvest rates that year. This may have been caused by the increased perching material provided during the rearing of 2017 increasing roosting behaviours in the Enhanced birds above that of the levels seen in 2016 to the point where Control birds began to copy the behaviour once they were brought together in the release pens. Improved foraging behaviours have been shown to be learnt via social transmission in hens and jungle fowl (Nicol, 2004), and Whiteside, Sage, and Madden (2016) showed that within a few weeks of release levels of perching behaviours of those pheasants reared without perching material had risen to match those reared with perching, proving that perching behaviours can be learned relatively swiftly. This effect of Control birds learning to roost swiftly in Year 2 may have occurred at Site 3 alone because it is the GWCT's Loddington Estate, where pheasant management is carried out to a far higher standard than at most shoots, such as by providing extensive roosting space for all the pheasants within each release pen. This in turn could foster the swifter transmission of roosting behaviours between Enhanced and Control pheasants if Enhanced pheasants were exhibiting more perching behaviours in Year 2 due to increased perching during rearing. This also indicates that because the differences in weight and heart mass were present in both years, that they were more likely driven by enhancements that could not be transmitted between Enhanced and Control pheasants post-release, namely improved diet during rearing which was consistent between years.

Although rearing birds under Enhanced conditions can improve harvest rates, this is likely dependant on certain aspects of management, including the date of release, overall shoot management, the provisioning of preferred habitats, and accompanying predator control. As such, it may be that only Large shoots operating extensive game management and Small shoots that benefit from the natural carrying capacity of the shot land benefit from such enhancements. The Shooting Benchmark Survey 2018 (Game and Wildlife Conservation Trust, 2018) collected data from 130 shoots that released a total of 1.6 million birds, putting the average release of participating shoots at 12,308 birds, and it is the rise of large commercial shoots that caused the 9-fold increase in pheasant release numbers between 1961-2011 to the current 39-57 million level (Parrott, 2015; Aebischer, 2019). These are exactly the kinds of high-density releases where Enhanced Rearing could lead to reduced release numbers, and they are also where the greatest concentration of negative effects are found, both ethically and environmentally (Sage, Ludolf and Robertson, 2005; Sage *et al.*, 2009; Fischer *et al.*, 2013; Capstick, Sage and Hoodless, 2019). Considering just these 130 shoots that partook of the survey, a saving of 16% on a harvest of 35% of the 1.6 million birds released could permit the release of 200,000 fewer birds annually, yet would result in a 1.5% increase the pheasant harvest.

The adoption of Enhanced Rearing is only feasible if it is economically viable.

This cost to procure timber battens to build the A-frame perches used in year 2 and the cost of buying live mealworm and the birdseed mix was calculated as £0.30 per bird when rearing Enhanced pheasants in sheds of 300 using the same material suppliers as used in our investigation. As all enhancement were carried out at the game rearer's premises and not at the shoots themselves, this cost would be consistent between shoots of any size so long as the pheasants were still reared in sheds of 300. The overall cost of rearing, releasing, and managing a pheasant is on average £12.41 per bird (Game and Wildlife Conservation Trust, 2018). This means that a potential 16% increase in pheasant harvests would be accompanied by only a 2.4% increase in cost. Also, although it could be argued that the decrease in weight gain might adversely affect the pheasant meat industry, this cost would be negligible considering that 46% of the gamebird meat is exported from shoot free of charge, 12% of shoots actively pay for carcasses to be collected, and average payments per bird are only between £0.20-£0.30 (Game and Wildlife Conservation Trust, 2018). Furthermore, it might be possible to market the Enhanced bird meat in a way that highlights its positive environmental and ethical aspects and thus support a premium price, such as has been seen in organic food with increasing uptake over the past decades (Lockie *et al.*, 2002). However, there may be other costs from Enhanced Rearing. Changes in morphology could result in changes in flight performance, affecting the sporting aspect of shooting. This will be investigated in Chapter 3 of this thesis. Rearing pheasants in a manner that improved their foraging ability or selectivity could also have additional impacts on invertebrate prey populations in the habitats within which the pheasants are released and forage. This aspect will be investigated in Chapter 4 of this thesis.

2.5 Conclusion

We have demonstrated that rearing pheasants under conditions that are more naturalistic can lead to an increase in their harvest rates, although this is only evident on shoots that release earlier or that release 0-600 and >2000 birds. This work confirms earlier, more limited studies that pheasant survival to harvest is affected by their early life experiences (Whiteside, Sage and Madden, 2015, 2016; Santilli and Bagliacca, 2017). Assuming, conservatively, that Enhanced Rearing could be applied to 20 million of the 39-57 million pheasants released each year (Aebischer, 2019), then improved survival to harvest of 16% would decrease the number of pheasants needed to be released annually by 3.2 million. In addition to reducing both the negative environmental impacts of high density releases (Sage, Ludolf and Robertson, 2005; Sage *et al.*, 2009; Capstick, Sage and Hoodless, 2019) and (at least some of) the accompanying ethical concerns over releasing gamebirds for shooting, this would result in an annual net saving of £34.67 million for the shooting industry as a whole when also taking into account the cost of Enhanced Rearing. Considering that 42% of commercial shoots made a loss in 2018 (Game and Wildlife Conservation Trust, 2018) such savings alone could be enough for the methodology to be widely adopted.

Chapter 3: Does enhanced rearing alter the flight performance of pheasants and does the flight performance of a pheasant impact the likelihood of being shot?

Abstract

Various morphological, developmental, and environmental factors can affect the flight performance of a bird. For recreational hunters who shoot flying birds, specifically driven pheasants, flight performance is of special interest as it is widely believed that hunters prefer to shoot pheasants deemed to be more challenging and safe, that is higher flying birds. Previous studies have shown that wild pheasants fly higher than pen-reared birds, and this preferable flight performance may be replicated by rearing pheasants under conditions closer to those of wild pheasants. We reared 2800 pheasants under either Control (matching normal commercial practice) or Enhanced (provided with perching and an enriched diet) conditions and assessed their flight performances (angle of ascent after being flushed from cover) during two shooting seasons on one commercial pheasant shoot. We asked: First, does being reared under Enhanced conditions affect flight performance? Second, did flight performance affect the likelihood of being shot? Third, does the relative flight performance of the pheasant population overall change over the course of the shooting season? Birds reared under Enhanced conditions exhibited improved flight performance. Pheasants with higher flight performance were more likely to be shot at the beginning of the shooting season but by the end of a season the birds with the highest flight performance were the least likely to be shot. Finally, the average flight performance of the pheasant population did not change significantly over the course of the shooting season. This implies that, despite flight performance affecting the

likelihood of being shot, the effect is not large enough to impact the average flight performances of the remaining pheasant population over the course of the shooting season.

3.1. Introduction

Within bird species various factors, such as fat content (Price, 2010) or cardiovascular capacity (Nespolo *et al.*, 2018), can alter flight performance, and such differences may arise because of differential early life experiences, especially for birds reared in captivity (Liukkonen-Anttila, Saartoala and Hissa, 2000). Examples can be seen with pheasants (*Phasianus colchicus*) bred from wild stocks flying both higher and for longer than their pen-reared counterparts (Robertson, Wise and Blake, 1993), wild northern bobwhites (*Colinus virginianus*) flying faster and further than their captive reared counterparts (Perez, Wilson and Gruen, 2002), and in wild greater prairie-chickens (*Tympanuchus cupido*) who have also been shown to fly further than their pen-reared counterparts (Hess, 2004). The Enhanced Rearing studied in Chapter 2 of this thesis outlines how the addition of perching material and improved diet led to overall greater harvest rates in pheasants as well as morphological changes. The primary aim of the enhancements were to more closely mimic the rearing of wild pheasants within the restrictions of commercial pheasant rearing, as wild pheasants survive better post-release than pen-reared birds (A. P. Leif, 1994), but these rearing alterations may have also affected flight performance.

The morphological effects of Enhanced Rearing were reduced mass gain over time and increased relative heart mass, breast muscle mass, and tarsus thickness. Differences in such morphologies might lead to differences in flight performance via several means. Most obviously, even small changes in mass have been shown to significantly impact flight performance, with an increase of 7% of mass decreasing flight speed by 30% in zebra finches (Taeniopygia guttata) (Metcalfe and Ure, 1995). Larger hearts can increase flight capacity by increasing blood circulation to flight muscles (Nespolo *et al.*, 2018). Stronger breast muscles can improve the ability for the rapid take off that is seen in the types of flight that pheasants carry out (Tobalske and Dial, 2000). Conversely, smaller pectoral muscles can in some cases lead to more efficient flight (Dietz *et al.*, 2007). As total body mass, relative breast muscle, and heart mass were morphological features affected by Enhanced rearing, it follows that they may have altered Enhanced pheasants flight performances.

If Enhanced rearing did affect flight performance, it has two potential consequences; one for our interpretation of the benefits of rearing and releasing Enhanced pheasants, and one for the shooting industry itself in terms of sporting quality.

Firstly, changes to flight performance could introduce errors in analysing harvested pheasants via tag returns from shot birds. This may occur in one of two ways. Previous studies have shown that higher birds are shot at preferentially when multiple birds are presented simultaneously (Peter A. Robertson, Wise, and Blake., 1993), but it is also likely that low flying birds are proportionally more likely to be hit as they are easier targets. If Enhanced Rearing does alter flight performance and flight performance affects harvest rates, this could alter the composition of the harvest to disproportionately favour either Enhanced or Control birds and may not reflect how many are actually surviving in the wild to the point of being shot. This would distort our findings in Chapter 2 where we calculated survival improvements to harvest by comparing numbers of shot birds. To address this, it is necessary to measure differences in flight performance between Enhanced and Control pheasants and how flight performance impacts the likelihood of being shot by those who partake in shooting (hereafter ‘guns’). Robertson, Wise, and Blake’s (1993) study into pheasant flight performance saw no significant differences between harvest rates of higher flying wild pheasants and lower flying pen-reared birds, implying that flight performance does not affected overall harvest rates. However, this may not be the case in our study as there are 24 years separating the two studies, over which time release numbers have significantly increased while harvest rates have decreased (Robertson *et al.*, 2017). This can be demonstrated directly by Robertson, Wise, and Blake’s 48.6% release/harvest rate compared to Chapter 2’s 18.3%, and such changes in the shooting industry may have also caused changes in shooting preferences. Additionally, this increase in release numbers has been driven by the rise of commercial shooting (Parrott, 2015; Game and WIldlife Conservation Trust, 2019), resulting in a broader participation of less experienced guns. This decrease in average skill levels might have also impacted shooting preferences. Because of these reasons, the finding of Robertson, Wise, and Blake (1993) should be retested within modern shooting conditions.

Secondly, changes in flight performance induced by our novel rearing methods could directly affect the actual sport of shooting. As there is a perceived preference to shoot higher birds (Whitby, 2017; Sporting Gun, 2018; Gentleman’s Journal, 2019), providing higher flying birds could increase the sporting enjoyment of the guns. Conversely, having lower flying birds could reduce this sporting enjoyment and result in reduced incomes for commercial shoots who adopt Enhanced Rearing. Additionally, if higher-flying birds are being shot preferentially, overharvest of them early in the season might lower the flight performance of the surviving pheasant population as a whole later in the shooting season. On commercial shoots, guns typically pay for the number of birds that they shoot, and as such may choose to pass up the chance to shoot a low bird in the hope that a more challenging high bird will be presented. This could mean that harvest rates are not maximised and some released pheasants do not fulfil the purpose for which they were bred, essentially being wasted.

To investigate any relationships between Enhance Rearing, flight performance, and likelihood of being shot, we first observed whether Enhanced Rearing alters pheasant flight performance, with the prediction that birds reared under Enhanced conditions that better matched wild rearing conditions would fly higher. We then observed the flight performances of the pheasant population as a whole over the course of the shooting season with the prediction that higher flying birds would be more likely to be hit than low ones. We then observed whether the flight performances of pheasants presented to the guns changed over the course of the shooting season regardless of whether the bird was hit or not. This was important because a shift in the relative proportions of differing flight performances would impact the numbers available to be shot and so could influence the likelihood of a particular flight performance score being shot at. It was our prediction that if preferential shooting of high birds was significant, it would leave predominantly low-flying birds later in the season.

3.2. Methods

3.2.1 Data collection

Data was collected on pheasant flight performance from the Game and Wildlife Conservation Trust's (GWCT) research site at Loddington over 2 years across 13 shoot-days. In 2016, Loddington released 500 pheasants reared under Enhanced conditions and 500 reared under Control conditions alongside 1500 other pheasants that were not part of my study. In 2017 this was increased to 800 Enhanced and 800 Control birds of the 2500 total. All birds released were males, in line with the GWCT stocking policy, and the guns were instructed to only shoot males. Briefly, Enhanced birds were reared in the same manner as Control birds with the addition of access to elevated perches from one week old and a diet of age-appropriate commercial feed pellets supplemented with 1% live mealworms and 5% mixed bird seed. For full details of the Enhanced rearing methodology, see Chapter 2. Enhanced and Control pheasants were marked using patagial wing tags to differentiate between treatments.

Driven pheasant shooting, such as that carried out at Loddington, is achieved by the guns standing in a line, separated from one another by 10-40m, across an area that the pheasants will be pushed towards. Each location where shooting takes place is known as a 'drive', and most shoot-days consist of between 5-8 drives. Once in position, beaters then walk through the habitat where the pheasants are likely located and push the pheasants into flight towards the line of guns. On larger shoots where many pheasants are present at a high density, pheasants frequently cluster under suitable shelter and so a group of them are disturbed together, constituting a 'flush', and hence several birds fly towards the guns simultaneously. On smaller shoots, the presence of fewer pheasants means that they often fly individually. Loddington would be classified as a larger shoot. Natural pheasant flight behaviour once flushed is to climb with a burst of energy at a steady angle for a few seconds until a maximum height is reach, whereupon they cease wing-beating, set their wings, and glide with occasional wing beats until landing.

On each shoot-day at Loddington we (AH) stood in a location that allowed for a clear side-on view of where the majority of pheasant would be flushed from on each drive in order to most accurately visually estimate the angle of incline of take-off and follow the pheasant's flight path. Flight performance was classified as one of four flight scores based on the average angle of climb the bird achieved once flushed before starting its glide, similar to techniques in Robertson, Wise, and Blake (1993). The four flight scores comprised angles of: 0-12.5° = 1, 12.5-25° = 2, 25-37.5° = 3, and >37.5° = 4. All scores were estimated visually and made blind to the identity of the bird, its rearing background, and whether it went on to be shot. All measures were made by AH to ensure consistency. Accuracy of scoring was confirmed in a separate truthing project by estimating the angle of clay pigeons thrown at known angles to mimic flushed pheasants. One hundred clay targets were scored which were thrown at an angle of ascent known to the trap operator but unknown to the scorer. Each clay was scored following the methods used to score the live bird flight. True Scores were then compared to Estimated Scores using a Spearman correlation test in R V3.6.1. Our Estimate Scores and the True Scores exhibited a strong correlation (S = 8700.1, P = <0.0001, rho = 0.948). The angle of assent was used as a metric for flight performance as steeper angles of incline require greater effort to achieve and the initial acceleration to achieve flight is greater than that used to sustain it (Berg and Biewener, 2010). As such, angle of assent allows for rapid scoring of individuals that can be easily repeated and is a viable measure of overall flight strength and performance.

Only the first pheasant from each flush was scored. Strong winds could have had an effect on pheasant flight performance (Liechti, 2006; Spear and Ainley, 2008), and so on any drive where winds were >15mph, no flight scoring was conducted. Once scored, the bird was visually tracked until either passing safely over the guns or being shot, with the bird's fate noted with its score. Any bird that had not begun its glide at the time of being shot was discounted, as its average angle of flight could have changed if it had continued its climb. For birds that were shot, we rapidly retrieved the carcass (so long as it was safe to do so) to check for tags to confirm their rearing condition. Over the course of two shooting seasons, we collected Flight Scores for 429 birds that were not shot and 505 birds that were shot, of which 60 of the shot birds were reared under Control conditions and 50 reared under Enhanced conditions. Data collection provided the following variables for the analysis. Flight Score = score of 1-4. Treatment = if the pheasant was tagged, whether it was Enhanced or Control. Fate = if the bird was shot (hit or escape). Days Since Release = the number of days between Loddington's pheasant release and the day the bird was shot. Year = if the score was taken in Year 1 (2016) or Year 2 (2017).

3.2.2 Data analysis

All statistical analysis was carried out in R version 3.6.1 (R Core Team, 2018) using the lme4 (Bates *et al.*, 2015), mgcv (Wood, 2011), gam (Wood, 2017), and MuMin (Barton, 2019) packages.

3.2.2.1 Does Rearing Condition affect flight performance?

This analysis included 110 flight-scored pheasants known from tags to have been reared under either Enhanced or Control conditions. A Generalised Additive Model was produced with Flight Score as the dependant variable and Treatment, Year, and their interaction as independent variables and Days Since Release used as a smoothed independent variable. A GAM was chosen because it integrated variable effects of Flight Score over time. Flight Score was able to be treated as an ordinal dependant variable by using the ocat family of model structures. This allowed us to account for the relatively continuous nature of each Flight Sore. This structure allowed for the relatively low number of Scores 1 and 4 to be incorporated into the model, it produced a single measurement on the overall effect of treatment between all scores, and it predicted likelihoods (0.0-1.0) of each Treatment scoring each of the four Flight Scores over the course of the shooting season. Model reduction was then carried out to removed non-significant independent variables and reduce model AIC, as reducing model AIC is considered an appropriate method of improving model accuracy (Akaike, 1974). Both Year and its interaction with Treatment were removed to produce a final minimal model with the lowest AIC. The final minimal model structure can be seen in Table 3.1.

3.2.2.2 Does flight performance affect the likelihood of being shot?

We tested whether fate (being shot vs. surviving the drive) was explained by an individual's flight score and whether this probability differed over the shooting season, which we tested by including Days Since Release and the interaction with Flight Score. We also included Year and its interaction with Days Since Release as a fixed factor to control for any differences in the birds or shooting abilities between years. The results of this model answer whether Flight Score affects the likelihood of a bird being shot. If there is a consistent effect of Flight Score predicting the likelihood of being shot over the entire shooting season, then it could lead to disproportionate representations of a particular or multiple Flight Scores within the harvest. However, such consistency may facilitate a correction factor that could be applied to tag records to account for any disproportionate representation. This model will not be able to differentiate if any effect of Flight Score on likelihood of being shot is driven by the preferences of the guns to shot at pheasants at a particular height or driven by their skill and ability at shooting pheasants of a particular height. This analysis included all birds scored regardless of their rearing origin, so we could include all 935 scores (1=n106, 2=352, 3=n345, 4=n132). A GLM was created with Fate as a binomial dependant variable, with the result being either Hit or Escaped. A GLM was selected over a GAM as it would produce single values for any of the relationships between Flight Score and Days Since Release, as opposed to using Day Since Release as a smoothing factor in a GAM, and these single values were considered more appropriate for direct comparisons. Unlike the previous model that was specifically designed to incorporate ordinal dependant variables, here Flight Score was an independent variable. As such, it was first added as an Ordered Categorical variable (in effect an ordinal variable). However, this did not change the model predictions or AIC when compared to adding it as a simple Categorical variable, merely the manner in which those results were presented in the model output. As treating the Flight Scores as Categorical allowed for a far easier descriptive comparison between scores, this was chosen for the analysis. A logit link function was used in the binomial model structure due to the relatively similar number of Hits (n = 488) and Escapes (n = 447). Model reduction was then carried out to removed non-significant independent variables and interactions to reduce model AIC. In this instance, the Dredge package was used due to the high number of independent variables and interactions.

3.2.2.3 Does the abundance of a particular Flight Score change over time?

The number of birds of each Flight Score from each shoot-day was divided by the total number of birds scored that day, producing a Flight Score Proportion for each Flight Score for each of the 13 shoot-days. This Flight Score Proportion was then used as the dependant variable in a LMER, where Flight Score and the interactions between Flight Score and Days Since Release were used as independent variables and Shoot-Day was the random effect. Again, treating the Flight Scores as Categorical as opposed to an ordinal Ordered Categorical did not change model predictions or AIC, merely the manner in which the results were presented in the output, and so for ease of descriptive comparisons in the results section, Flight Score was considered as a Categorical variable. Year and its interactions were also added to the model but then removed after being shown to have an insignificant effect and to increase model AIC. Model Structure can be seen in Table 3.1.

Model Name	**Dependant Variable**	**Independent Variables**
Flight Treatment GAM	Flight Score (Ordinal)	Treatment
		Smoothed: Days Since Release
Shooting Likelihood GLM	Fate	Flight Score (Categorical)
		Days Since Release
		Year
		Interaction: Score, Days Since Release
		Interaction: Year, Days Since Release
Time-Flight Performance LMER	Flight Score Proportion	Flight Score (Categorical)
		Interaction: Flight Score (Categorical), Days Since Release
		Random Effect: Shoot-Day

Table 3. 1 Final model structures for the three investigations after the complete models were reduced to those with the lowest AIC.

3.3 Results

3.3.1 Does Treatment affect Flight Performance? – Flight Treatment GAM

Pheasants reared under Enhanced conditions flew higher than those reared under Control conditions (Estimate = 0.8359, P = 0.0282, Fig 3.1) and this effect was consistent across the two years of study (Estimate = 0.263, P = 0.558).

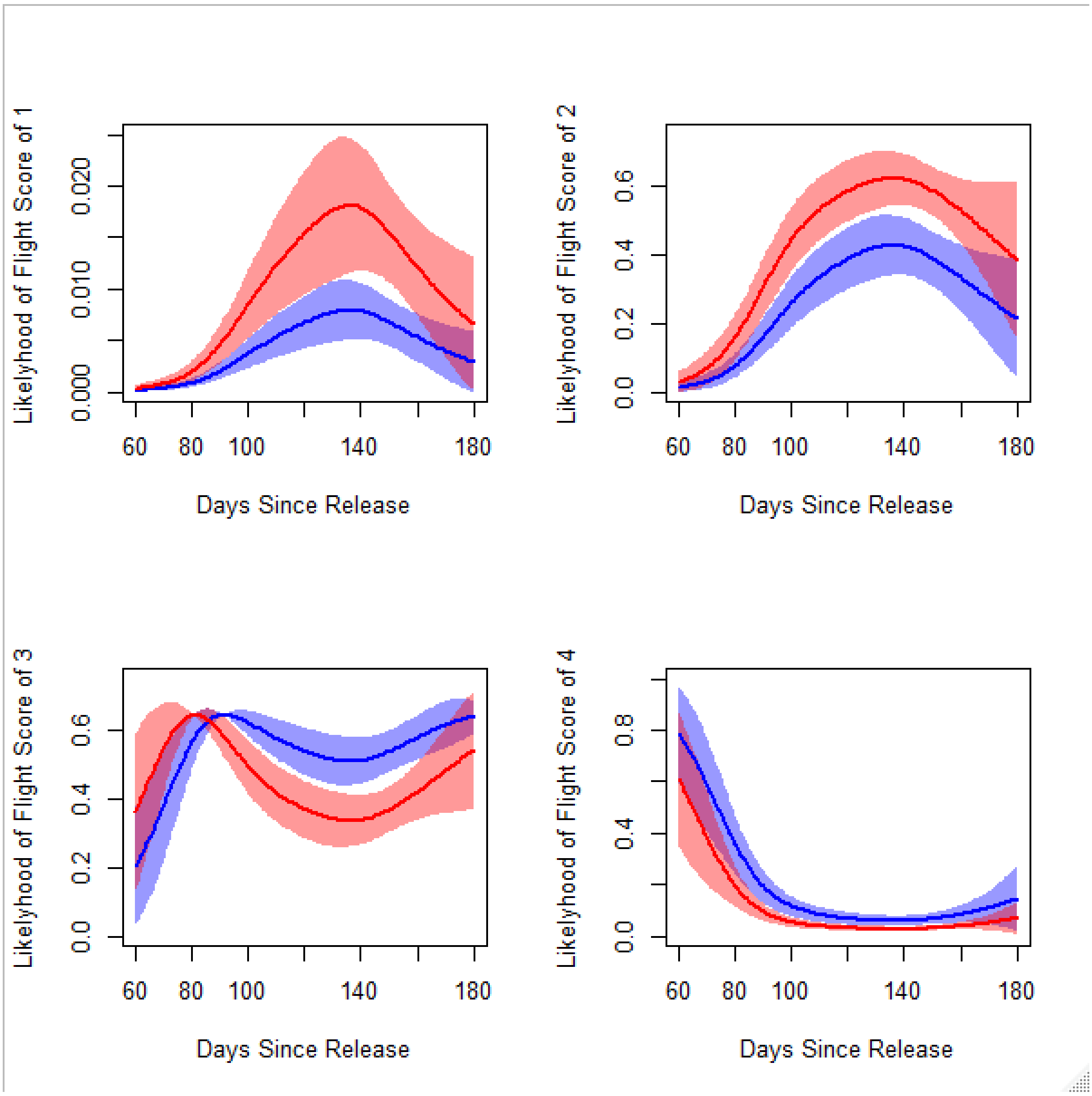

Figure 3. 1 The likelihood and standard errors of a bird exhibiting a particular Flight Score as the shooting season progressed, depending on the conditions under which the bird had been reared, Control birds = RED Enhanced birds = BLUE.

3.3.2 Does flight performance affect the likelihood of being shot? - Shooting Likelihood GLM

At the start of the shooting season, low birds (Score 1) were less likely to be shot, but birds scoring between 2-4 were shot in equal measure (Fig 3.2). Score 4 (the intercept), Score 3 (Estimate = -1.774, P = 0.073) Score2 (Estimate = -1.700P=0.093), Score 1 (Estimate -5.025, P = <0.001). In 2016, as Days Since Release increased, the likelihood of hitting the pheasants decreased across all flight scores, with Score 4 decreasing the most per day (Estimate = -0.043004, P = <0.001), then Score 2 (Estimate -0.028, P = 0.054), then Score 3 (Estimate -0.027, P = 0.046), and Score 1 the least (-0.008, P = 0.001). (Figure 3.2). In 2017, the likelihood of successfully shooting pheasants exhibiting any particular Flight Score relative to any other did not change from Year 1. However, at the start of the shooting season, birds exhibiting all scores were equally less likely to be shot than in Year 1 (Estimate -5.025, P = <0.001), but their likelihood of being shot then equally increased over time compared to Year 1 (Estimate = 0.040, P = <0.001). (Figure 3.2).

Consequently, in both years the lowest flying birds (Score 1) were least likely to be shot at the beginning of the shooting season, but the highest flying birds (Score 4) were least likely to be shot by the end.

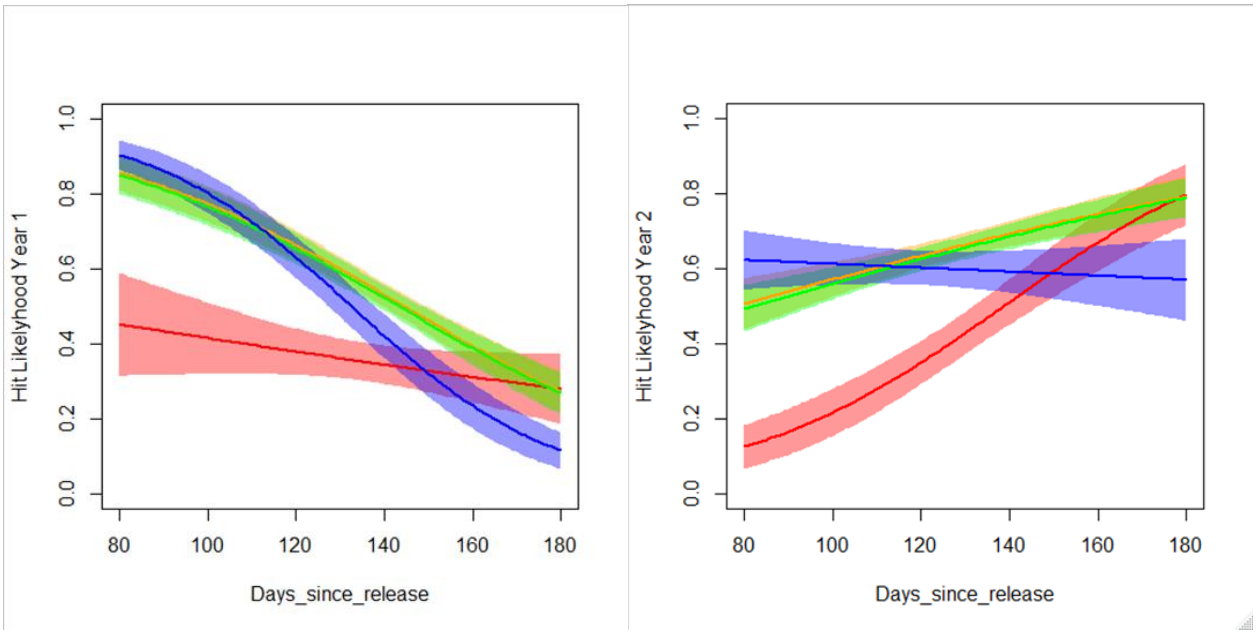

Figure 3. 2 Predicted mean likelihood and standard errors of each Flight Score being shot over the course of the shooting season of Year 1 and Year 2 with 0.0 = not shot and 1.0 = shot. Score 1 = Red, Score 2 = Orange, Score 3 = Green, Score 4 = Blue.

3.3.3 Does the abundance of flight scores change over the shooting season? Time-Flight Performance GLM

The distribution of each Flight Score Proportion did not change significantly across the shooting season: Score 1 (Estimate = -.00137 , P = 0.0835), Score 2 (Estimate = 0.00105 , P = 0.183), Score 3 (Estimate = 0.000398, P = 0.610), Score 4 (Estimate = -0.0000724, P = 0.926). (Fig 3.3). Mean values of each Flight Score Proportion were Score 1 = 0.099, Score 2 = 0.361, Score 3 = 0.372, Score 4 = 0.167.

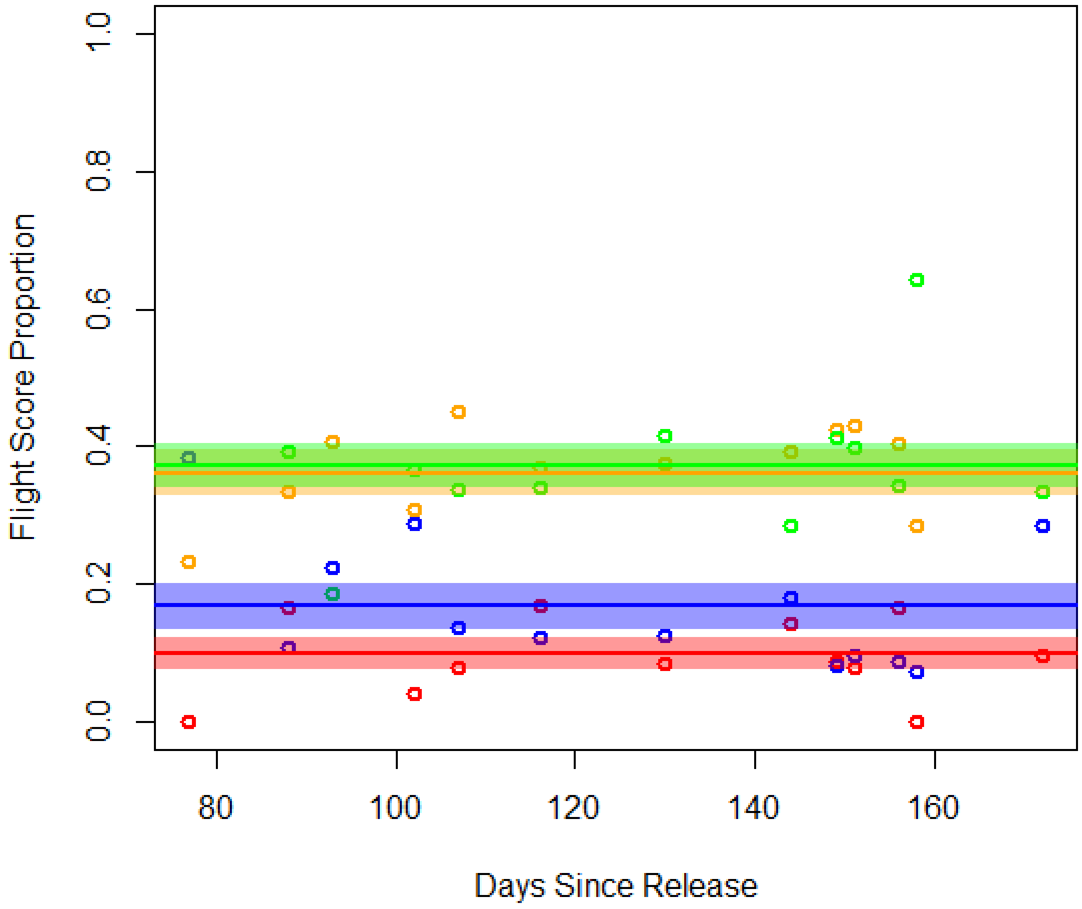

Figure 3. 3 Total numbers of each flight score as a proportion of all scored birds over the course of the shooting season (points) and mean of each Flight Score Proportion across the shooting season with standard errors (lines) , with a proportion of 1 = 100% of scored birds belonging to that specific Flight Score on that Shoot-Day. Score 1 = Red, Score 2 = Orange, Score 3 = Green, Score 4 = Blue.

3.4. Discussion

Pheasants reared under Enhanced conditions, designed to better match natural 'wild-type' birds (Chapter 2) flew at a steeper angle when flushed during driven game shooting. Whilst the likelihood of a bird being shot is increased with higher Flight Scores at the start of the shooting season, as the season progresses this effect disappears such that at the end of the season the highest-flying birds were those least likely to be shot. Due to this shift, it is unlikely that higher or lower flying birds would have been consistently disproportionately harvested over the entire shooting season. The proportion of birds flying with each Flight Score did not differ across the season in either year. This shift in the likelihoods of individual Flight Scores being shot did not occur because of changes in the prevalence of those Flight Scores within the population, because the proportion of birds flying with each Flight Score did not differ across the season in either year.

Enhanced Rearing produced birds that consistently exhibited improved flight performance scores across both years, perhaps because such Enhanced birds exhibited slower rates of mass gain and larger heart mass relative to body size in both years (Chapter 2). Prolonged flight, as opposed to flight designed for rapid predator avoidance (Askew and Marsh, 2002), is reliant on a constant flow of oxygenated blood to the flight muscles and could benefit more from the larger heart mass relative to body mass than it would by simple increases in breast muscle (Butler, 1991; Nespolo *et al.*, 2018). Support for this is shown by Enhanced birds having larger relative breast muscles in 2016 alone but larger relative heart mass in both years (Chapter 2), corresponding to higher Flight Scores being consistent in both years. Additionally, the lighter mass over time of Enhanced birds (Chapter 2) which was again consistent between years would put them closer to their wild counterparts, which also weigh less than standard pen-reared birds and also fly higher (Musil & Connelly, 2009; Robertson, Wise, and Blake, 1993).

The flight performance of birds is expected to affect how attractive they are to shoot (at) and also affect the probability with which they can be shot, and thus flight performance may affect their representation in any harvest records. I found mixed support for this assumption. Robertson, Wise, and Blake (1993) found that guns preferentially shot at higher flying birds. I confirmed this at the beginning of the shooting season in my study. However, by the end of the shooting season we found that the effect of flight performance on likelihood of being shot had shifted, with the highest-flying birds now being the least likely to be shot. An example would be that in Year 1, on 80 days after release (the beginning of the shooting season) the likelihood of a Score 4 being hit was predicted as being 90.5%, but by 180 days after release the likelihood of Score 4 being hit was predicted as being 11.5%. This is despite the proportion of Score 4 within each shoot's sample (average of 16.7%) not changing significantly over the course of the shooting season.

Additionally, although the overall likelihood of being shot over time differed between years, the difference in likelihood of one Flight Score being shot when compared to another Flight Score did not differ between years. Robertson, Wise, and Blake's (1993) study was also conducted over the course of the entire shooting season, but they do not appear to have tested to see if the relationships they found changed over the course of that shooting season. This makes it unclear if the shift in the likelihood of a particular Flight Score being shot over time that is shown in our study has developed over the 24 years since Robertson, Wise, and Blake’s (1993) study, if it was present to some degree before but remained untested, or if it was specific to this particular site.

A possible explanation for this shift over the shooting season would be that at the beginning of the shooting season there were simply more pheasants available to shoot at, allowing guns to preferentially pick their birds. Although the relative Flight Scores of the population as a whole did not to change over time, the actual number of birds presented to the guns would reduce over the season due to both harvesting and natural attrition (Sage *et al.*, 2018), reducing the total pool of higher flying birds to shoot at if the guns wished to shoot the same number of birds in total as they did at the beginning of the season. This would explain why Scores 1, 2, and 3 converge in likelihood of being shot by the end of the shooting season, but it would not explain why the highest flying birds at Score 4 become the least likely to be shot at the end of the season. Another possible explanation would be that most shoots, primarily those commercial in nature, rely solely on a fresh injection of birds released the following year (Bicknell *et al.*, 2010) and have no incentive to conserve stocks over winter/spring once the hunting season has ended. Consequently, they often encourage their guns to ‘clear-up’ what birds remain towards the end of the season to reduce the cost of maintaining the birds when very few would survive to contribute to the next season’s harvest (Turner, 2007). This practice could shift preferences away from the harder to hit higher birds and towards shooting any lower bird that could be hit safely by the end of the season.

Biases in sampling techniques are not uncommon in the study of animals in the wild, such as animals that are trapped being disproportionately bold (Carter *et al.*, 2012). This can potentially lead to errors in data analysis, particularly when those individuals within groups most likely to be sampled share specific morphological or behavioural traits in addition to that which increased the likelihood of their initial sampling (Biro, 2013). Methods for dealing with such sampling errors exist, such as incorporating heterogeneous capture probabilities into models to offset any biases (MacKenzie and Kendall, 2002) (MacKenzie and Kendall, 2002). However, before these corrections can be added, the scale of the sampling bias, if indeed there is one present, must be established.

In the case of this study, if Enhanced birds were flying higher and higher-flying birds were consistently shot preferentially, it might skew harvest rates such as those collected in Chapter 2. However, the preference for shooting the highest-flying birds in our study was not consistent and in fact inverted so that by the end of the season the highest fliers were least likely to be shot and the three lower Flight Scores were all equally as likely to be shot. This reduces the likelihood that higher flying birds may have contributed disproportionately to the harvest.

The fact that the switch between Score 1 and Score 4 becoming the least likely to be shot did not occur until after halfway through the shooting season might imply that Score 4 harvests could be positively skewed. However, there are several arguments against this. The first is that the instances of Score 1 (n 106) and Score 4 (n 132) were far lower than the instances of Score 2 (n 352) and Score 3 (n 345). This means that the Score 4 likelihood dropping below Scores 2 and 3 in the first half of the shooting season will likely have a greater effect on skewing results against Score 4 than Score 4 gained from remaining more likely to be shot than Score 1 for longer into the season. In short, the lower instances of Scores 1 and 4 mean that they would have had a far smaller impact on any potential skewing of results when compared to the far more numerous Scores 2 and 3 which remained almost identical.

Another argument against the higher-flying Enhanced pheasants being disproportionately favoured is that any disproportionate favouring should have caused differences between Enhanced harvest rates of the Large and Small shoot classifications in Chapter 2. This is because the concept of ‘picking’ which birds to shoot is only applicable if there are many pheasants to choose from, and on Small shoots far fewer pheasants are released and pheasants tend to be flushed singly or in very low numbers, with the guns almost always outnumbering the birds available to be shot. If changes in shooting preferences had caused a significant discrepancy in the results of Chapter 2, then Enhanced harvests should have been proportionally higher on Large shoots where birds could be ‘picked’ than they were on Small shoots where all safe birds presented to the guns are typically shot at. This was not the case. Additionally, Robertson, Wise, and Blake (1993) also showed that, despite the preferences to shoot higher birds, the harvest rates of those birds that flew higher was not significantly greater than those that flew lower. Comparatively, this result should be even more pronounced in our study, where the preferences for the highest birds were only present at the start of the shooting season.

The effects of flight performances on likelihood of being shot were not only inconsistent but appear to reverse. This means that a single ubiquitous correction factor that would account for Enhanced pheasant’s higher flight performance cannot be applied. However, due to the reversal of the effect of flight performance on likelihood of being hit, we feel that it is unlikely that a correction factors is even required.

We also showed that the Flight Score Proportions did not alter significantly over time despite changes over time in the likelihood of particular Flight Scores being shot. First, this means that there were no changes in the abundance of any Flight Score over time that may have impacted the likelihood of particular Flight Scores being shot preferentially. Second, this means that shoot managers can provide a standardised mix of different bird heights consistently across the season and could also allow them to more efficiently plan which drives to use.

3.5. Conclusion

Enhanced rearing increased pheasant flight performance, producing birds that take off at a steeper angle and thus are expected to fly higher. This improved performance, likely facilitated by the Enhanced birds being lighter and with relatively larger hearts, is likely to be desirable to those both managing shoots and those carrying out shooting themselves. After personal correspondence with various game keepers and figures within the shooting industry, the production of higher-flying birds alone was enough to encourage the Enhanced rearing methodology, showing that this unforeseen desirable effect may make Enhanced rearing more likely to be adopted. It is a widely held belief that producing higher flying birds makes for better sport (Whitby, 2017; Sporting Gun, 2018; Gentleman's Journal, 2019). However, our findings show that this often-reported preference for higher birds is not supported by the actual actions of those carrying out shoots, though whether this is from a change in preference or ability we cannot determine. If the shift in the likelihood of particular flight scores being shot is due to changes in shooting preferences, as opposed to shifts in their ability, knowing about this shift could also allow shoots to reorganise their drives to better suit these preferences and increase participant's enjoyment, with pheasants flushed from higher drives at the beginning of the season and lower drives towards the end. The possible shift in shooting preferences and the fact that average flight score distributions don't change over the course of the shooting season also removes any perceived need for shoots to release higher numbers of pheasants to ensure that there are still higher flying birds present at the end of the season. There is also an additional benefit from the shift in the likelihood of particular flight scores being shot. At the Loddington shoot, where the study was carried out, or on other shoots where there may be a significant population of wild-born pheasants, these wild birds may be disproportionately likely to survive a shooting season compared to pen reared birds. Wild pheasants die of natural causes at a reduced rate over time than pen-reared birds (Leif, 1994), meaning that by the end of the shooting season a higher proportion of the available birds are of wild stock than at the beginning. Because wild birds fly higher (Peter A. Robertson, Wise, and Blake., 1993) and because the likelihood of shooting a higher bird is lowest at the end of the season, the change in shooting preferences would disproportionately favour wild birds to survive to the end of the shooting season and into the breeding season, further bolstering populations of wild pheasants.

Chapter 4: The impact of pheasants on the invertebrates and habitats within the release pen

Abstract

Each year tens of millions of pheasants (*Phasianus colchicus)* are released into woodland release pens to acclimatise the birds to the natural environment before being given access to the surrounding habitat. This study investigated immediate effects of pheasant releases on invertebrates and habitats in and immediately around release pens and asked if releasing pheasants with improved foraging abilities (Enhanced pheasants) might cause additional negative effects. The interior fauna and flora of forty-nine release pens were compared to pen exteriors via pitfall trapping and habitat surveys prior to, 4 weeks after, and 9 weeks after pheasant release. Due to significant differences in overall invertebrate abundance between the two years of the study, the different effects of pheasant releases on high or low invertebrate populations could be investigated.

Prior to release, there were no differences between invertebrate populations inside or 25m outside the pen in either year. When invertebrates were more abundant, total invertebrate biomass and slug and detritivore counts were lower inside the pen 4 weeks post-release. When invertebrates were less abundant, the main effects were only seen 9 weeks post-release, with higher total invertebrate biomass and total invertebrate, slug, and beetle counts within pens.

Chronic effects of releasing pheasants in previous years caused pen interiors prior to release to have higher bare ground. Interior bare ground increased further

and ground vegetation decreased both 4 and 9 weeks after pheasant release. Prior to release, higher density releases in previous years lowered pen interior invertebrate biomass, lowered detritivores counts both inside and outside of pens, and raised slug counts both inside and outside of release pen. Releasing Enhanced pheasants showed no additional negative effects on invertebrates or habitats than are caused by the release of traditionally reared pheasants.

In conclusion, the effects of pheasants on invertebrates within the release pen (be they negative or possibly positive) appears largely dependant on the overall abundance of invertebrates, but chronic effects on invertebrates that are present prior to release, both within and outside the release pen, appear driven by the density at which pheasant were released in previous years.

4.1 Introduction

The release of pheasants (*Phasianus colchicus*) and their associated management can have a wide and mixed range of effects on native flora and fauna in and around their woodland release sites (Mustin et al 2017). For birds, tit species are less abundant in pheasant release woods while woodpigeons (*Columbia palumbus*), warblers, finches, and ground feeders are more abundant (Davey, 2008; Draycott, Hoodless and Sage, 2008). For mammals, pheasant releases are correlated with lower common shrew (*Sorex Araneus*) populations while wood mice (*Apodemus sylvaticus*) are more abundant (Davey, 2008). For invertebrates, butterflies are found at significantly higher numbers in pheasant release woodlands while ground-active invertebrate biomass and larger carabid numbers are found in lower numbers (Robertson, Woodburn and Hill, 1988; Pressland, 2009; Neumann *et al.*, 2015). When focussing specifically on rides within pheasant release woods, game management had no effect on butterfly abundance (Capstick et al. 2019b).

In general, the management of woodlands for pheasants is beneficial for wildlife (Robertson, Woodburn and Hill, 1988; Draycott, Hoodless and Sage, 2008), while the release of pheasants themselves tends to have negative effects (Sage *et al.*, 2009; Capstick, Sage and Hoodless, 2019). These effects occur close to where birds congregate, such that areas nearer to pens have increased bare ground and fewer stable perennials (Sage *et al.*, 2009), evidence of increased dominance of species associated with high-nutrient soil within release pens (Capstick, Sage and Hoodless, 2019a), and lower average floral species diversity within release pens (Sage, Ludolf and Robertson, 2005). Although highly localised, these negative effects are likely to be widespread nationally, with an estimated 1 in 12 woodlands in the UK believed to contain pheasant release pens (Sage, Ludolf and Robertson, 2005). The extent of the negative effects may be influenced by the density of pheasant releases, with pen stocking densities of no more than 0.07 birds/m^2 recommended by the Game and Wildlife Conservation Trust (GWCT) to prevent chronic habitat degradation within pens (Sage and Swan, 2003). Degradation of hedgerows within 250m of release pens is associated with releases greater than 1000-1500 birds (Sage *et al.*, 2009), stocking densities above 0.1 birds/m^2 causes shifts in pen floral community (Sage, Ludolf and Robertson, 2005), and negative effects such as shifting in floral communities and soil nutrient build-up persist for more than 10 years within abandoned release pens with stocking densities >0.1 birds/m^2 (Capstick, Sage and Hoodless, 2019a).

These negative effects on flora may extend to woodland fauna populations within or near the release pen. The wild pheasant's diet during their first few weeks of life is comprised almost exclusively of invertebrates (Warner, 1979), and variations in arthropod densities can account for 75% of the variation in pheasant chick survival (Hill, 1985). After these first weeks, their natural diet begins to vary to include seeds and plant material (Dalke, 1937), but invertebrates still feature within the diet (Hoodless *et al.*, 2001; Doxon and Carroll, 2010). Captive-reared pheasants are typically 6-8 weeks old at release. While they are provided with feed by game keepers (grains and pellets), they may also forage on natural fauna and flora. Around 39-57 million pheasants are released each year into UK woodlands (Aebischer, 2019), and consequently even low individual levels of predation could affect invertebrate populations. Limited negative long-term effects of high-density releases have also been demonstrated. Within release pens stocked at >1000 birds/ha, spring populations of large carabids were lower within the release pen (Neumann *et al.*, 2015). There was also a general shift in invertebrate communities away from woodland assemblages and towards arable assemblages, but overall abundances of other invertebrate taxa differed little between pen interior and exterior in spring (Neumann *et al.*, 2015). However, that particular study was conducted in the spring, by which time released gamebirds have typically left the release pen and indeed only around 16% of them are still alive after the winter hunting season (Turner, 2007). Therefore, effects of their predation or disturbance at this time may be less noticeable than when they were initially released into the pen in late summer, although one study considering invertebrate biomass at this time found no overall decreases immediately following release (Pressland 2009).

Negative impacts upon invertebrates within the release pen may be driven directly, by predation, or indirectly, by changes in habitat structure caused by the pheasants, as has been seen in grassland invertebrates from the effects of grazing sheep (Bromham et al, 1999). Prior to release, release pen interiors have increased bare ground, lower vegetation below 50cm, and increased phosphate and potassium levels in the soil compared to comparable areas of woodland without release pens (Sage, Ludolf and Robertson, 2005). Increased soil nutrients lead to floral communities of non-woodland specialist outcompeting the woodland specialists, which then alters the invertebrate community to more closely match the ground flora associated with woodland edges and arable fields (Neumann *et al.*, 2015). Such habitat perturbations may have long term effects on invertebrate populations, with woodlands that hold release pens having lower invertebrate biomass than non-releasing woodlands overall (Pressland, 2009). This hints at chronic negative effects that accumulate over time, although these differences may simply reflect differences in the woodlands being chosen as the site of release pens.

Direct effects of predation by pheasants on invertebrate prey may be exacerbated by the feeding strategies of the released birds. Recent work has attempted to rear pheasants in more naturalistic conditions in order to improve both individual welfare and survival post-release (Whiteside, Sage and Madden, 2015). They fed young pheasants with a diet containing live invertebrates which increased their ability to catch novel invertebrate prey and their diet diversity when in the wild and may explain their better survival after the shooting season. The Enhanced Rearing technique that has been tested in Chapter 2 also provided pheasants with live invertebrates during rearing. Enhanced Rearing has shown positive effects on harvest rates, but if these Enhanced pheasants are widely released and are more successful predators of invertebrates in the release pen, the negative effects on invertebrates may be greater than anticipated.

Therefore, we tested how invertebrate populations in release pens were affected by the release of Enhanced and standard pheasants. Because invertebrate populations are highly seasonal and may be ephemeral, changing in their size across time, simply comparing pre- and post-release measures may be hard to interpret. Instead, comparing measures made simultaneously within and outside the pen may be more informative. Invertebrate populations are highly susceptible to climatic conditions (Rae *et al.*, 2006). Differences in these conditions between years might also distort the relationships between pheasants and the invertebrate communities. An example would be hotter and drier years resulting in increased total invertebrate biomass (Morecroft *et al.*, 2002), possibly reducing the proportional effects of pheasant predation. Therefore, we compared invertebrate abundance within and outside of release pens immediately prior to release, 4 weeks after release when the birds were typically still within the pen, and 9 weeks after release when birds had largely dispersed out of the pen into the surrounding landscape. We explored whether any effects were more likely to be driven by the density at which pheasants were released, with the prediction that effects would be greater when more birds were released into a pen. We considered whether the predatory behaviour of the pheasants was an important determinant of changes in invertebrate populations, with the prediction that pens holding birds reared under Enhanced methods with experience of catching live prey would host greater invertebrate decreases. We then explored whether changes in invertebrate populations could be explained by indirect effects of the released pheasants altering vegetation structure which in turn may affect invertebrate populations. Finally, we explored whether these effects were consistent across two years. Given the paucity of prior research, we made no predictions as to which taxonomic groups would be especially affected, but rather consider this to be an exploratory study in which we initially looked at overall invertebrate populations and then refined our analyses, focussing on some common invertebrate groupings.

4.2 Methods

4.2.1 Study area

We monitored 49 pheasant release pens across 12 sites in Herefordshire and Worcestershire and 1 additional site in Leicestershire across 2016 and 2017. Some pens were surveyed in both years, resulting in a total of 65 pen surveys. The areas surrounding the release woods were predominantly arable or pastoral fields. Stocking density of the release pens ranged from 0.0216 birds per m^2 to 0.731 birds per m^2, with a mean of 0.257 per m^2 (Fig 4.1). The stocking density (Density) of each pen was calculated by dividing the number of birds released in each pen by the pen area (m^2) calculated using a GPS (Garmin Etrex Handheld GPS). Twenty one of the release pens were stocked with traditionally reared pheasants only, while the remaining 28 were stocked with birds reared under Enhanced conditions comprising 50% of the released birds in 22 pens, 40% in 3 pens, 33% in 1 pen, 18.18% in 1 pen, and 100% in 1 pen. Briefly, Enhanced birds were reared with access to elevated perches from one week old and a diet of age-appropriate commercial feed pellets supplemented with 1% live mealworms and 5% mixed bird seed. For full details of the Enhanced rearing methodology, see Chapter 2.

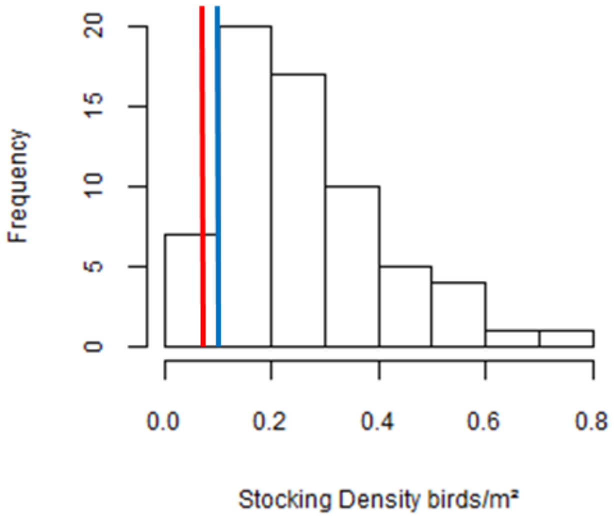

Figure 4. 1 Frequency of stocking Densities of release pens in this study in birds/m^2. Red line indicating GWCT recommended pen stocking density (Sage and Swan, 2003). Blue line indicating stocking densities that above which point can alter floral composition and still affect pen habitat 10 years after the pen is no longer in use (Capstick, Sage and Hoodless, 2019).

4.2.2 Study design

At each release pen, we conducted three surveys. At each survey, we conducted a habitat survey (see below) followed by pitfall trapping to sample inverebrate populations from inside (Interior) and outside (Exterior) of release pens. Survey 1 was conducted 2-4 weeks prior to pheasant release between 1 July and 19 August 2016 in Year 1 and 5 June and 14 August 2017 in Year 2. This allowed us to determine baseline differences in invertebrate populations between Interior and Exterior transects prior to pheasant releases. Survey 2 was conducted 4 weeks after pheasants had been released into the pens between 12 August and 30 September 2016 and 26 July and 30 September 2017, and during which time the pheasants typically remained entirely within the pen. This allowed us to explore the relationship between Interior and Exterior invertebrate populations and habitat scores compared to the baseline established in Survey 1. Survey 3 took place 9 weeks after the initial pheasant release between 16 September and 29 October in Year 1 and 6 August and 4 November in Year 2, by which time pheasants had typically dispersed out from the pen into the surrounding landscape. Due to logistical issues, we were unable to conduct Survey 3 at 6 release pens in 2016. We collected all three surveys from all pens in 2017.

4.2.3 Invertebrate surveys

Neumann et al's (2015) and Oliver and Beattie's (1996) methodologies formed the basis for our invertebrate sampling, with surface activity of invertebrates assessed using transects of pitfall traps. A transect consisting of five Interior traps was placed along the most central point within each release pen while an Exterior transect of five traps was placed 25m outside of the release pen parallel to the pen fence. In the first year (2016) we were concerned that local wildlife, particularly badgers, might disturb pitfall traps outside the pen, so we added an extra trap to each Exterior transect. Subsequently, this did not generally occur in that year, so we only placed 5 traps on Exterior transects in the second year (2017). Due to the small size of many of the release pens only 5m spaces were left between traps instead of 20m recommended by studies such as Woodcock (2005). This could have potentially resulted in over-trapping of local invertebrate populations and trapping itself decreasing invertebrate abundances (Ward, New and Yen, 2001). However, as this 5m distance was standardised between Interior and Exterior transects, any negative consequences should have been equal across locations. As many of the woodlands within which the release pens were located were also relatively small, with the smallest at ~2700

m^2, the Exterior transects were placed 25m from the release pens to ensure that the same woodland was surveyed. Although this close proximity increased the likelihood that the Exterior transects would be directly affected by the relatively nearby release pens, it also minimised potential variation in additional variables between Interior and Exterior transects (e.g. soil moisture, flora composition, topography, etc). All traps that were disturbed or destroyed by wildlife between surveys were replaced within a metre of the original site for subsequent surveys to ensure consistency.

Pitfall traps consisted of buried plastic cups (200ml) with the lip level with the soil. Covers were placed 3-5cm above each pitfall trap to prevent rainfall flooding samples and to deter other animals from scavenging each trap's contents. Each trap was filled to one third with a liquid comprising 89.05% water, 10% ethylene glycol and 0.5% Morrisons own-brand washing liquid. The traps were not baited. The traps were typically left for 7 days before collection. All trap contents from a single transect were pooled together. Samples were washed and sieved after collection to separate invertebrates from detritus and additional unwanted organic matter. The number of traps that survived each survey varied because of damage by wildlife, and some transects had to be collected on either six or eight days after being placed, rather than the standard seven, for logistical reasons. Therefore, we standardised each Invertebrate Measure by correcting for trapping effort per transect, using Invertebrate Measure/per trap/per day for the analysis.

We condensed our catch data from the pitfall traps into six Invertebrate Measures. We used the Total Biomass and Total Count of all individuals captured as a crude indicator of the entire invertebrate population. We then used counts for four common taxonomic groupings to allow us to investigate whether pheasants had differential impacts on particular invertebrate populations. These populations were primarily chosen because previous research (Neuman et al, 2015) showed that pheasant releases reduced the abundance of larger carabids and increased the abundance of spiders and woodlice. Additionally, little if any research has been previously carried out on the effect of pheasants on slug populations, so slugs were also specifically investigated to expand the current knowledge base. Slugs are of particular interest as they are a major farmland pest (Martin, 1991; Frank, 1998; Newzeland, 2002), and as pheasants are largely released in and around arable land, any effect that pheasants might have on slugs could be directly beneficial or detrimental to farming. As such, the populations that were separately counted were: Slugs (*Gastropda,* excluding snails), Beetles (*Coleoptera*), Arachnids consisting of spiders and harvestmen (*Arachnida*), and Detritivores consisting of woodlice and millipedes (*Oniscidea* and *Diplopda*).

4.2.4 Habitat surveys

We estimated habitat cover within a 10m radius of the central trap on each transect considering categories of: Bare Ground (exclusively exposed soil), Ground Vegetation (flora of a height 0-1m excluding mosses), and Shrubby Cover (vegetation between 1-2m). Each habitat classification was scored independently of the others, and as mosses and ground detritus (deadwood, manmade waste, etc) were not counted and the presence of Shrubby Cover effectively made the survey areas 3-dimensional, the combined percentage covers of all three classification for each transect do not equal 100%.

In Year 1, these habitats were visually classified on a scale of 1-4: 1 = (<5% habitat cover), 2 = (5%-30% habitat cover), 3 = medium (30%-60% habitat cover), and 4 = high (60%-100% habitat cover) in line with the Game and Wildlife Conservation Trust's pheasant release pen surveying method used for the National Game Marking Scheme, as this method had been previously used before by the surveyor (AH) and has been shown to produce reliable and repeatable results. In Year 2, this scoring methodology was altered to a rough estimate of direct percentage cover to provide a finer scale of accuracy for each percentage cover score. To make these measures comparable between years, Year 1 scores were converted to rough percentage covers at the midpoint between their score bands resulting in: 1 = 2.5%, 2 = 17.5%, 3 = 45%, and 4 = 80%. These results formed the three % Habitat Score variables.

We confirmed that our visual habitat estimates were accurate by directly quantifying ten 1x10m woodland transects using a 1x1m quadrat to measure cover of each type with a precision of 5%. Prior to conducting each transect, we (AH) visually estimated cover using the methods above for the transect as a whole. We then correlated our estimates against our actual measured percentages for each of the four cover types. Each of our estimates was strongly positively correlated with our measures (Bare Ground: R = 0.907, N = 10, P < 0.001; Ground Vegetation: R = 0.913, N = 10, P < 0.001; Shrubby Cover: R = 0.944, N = 10, P < 0.001).

4.2.6 Statistical analysis

All analyses were conducted in R version 3.6.1 (R Core Team, 2018) using the lme4 (Bates et al, 2015) and MuMIn packages (Barton, 2009). Generalised Linear Mixed Effect Models with a Gamma distribution and Log link function were used to analyse each Invertebrate Measure. Pen Identity was included as a random effect to ensure that Interior and Exterior scores for the same pens were matched. Gamma distributions were used because, despite the raw data appearing to be closer to an asymmetrical inverse gaussian distribution. This strong asymmetry was caused by some transects having collected far greater numbers of invertebrates than others. However, when these larger samples occurred they did so at the pen scale, with the Interior and Exterior samples of the same pen matching much more closely relative to one another. The addition of the random effect into the model design linked the results of each individual pen, reducing any effect of asymmetry in the data distribution and allowing for the effective use of a gamma distribution in the model family. Additionally, when an inverse gaussian family was used the models consistently failed to converge and produced results with far higher AIC values. Non-convergence rarely occurred directly within the Gamma distributed models, but near-non-convergence was still an issue. Rescaling variables can at times reduce this issue, but doing so here either significantly increased model AIC, increased non-convergence, or produced negative variables that the Gamma model structure could not analyse, and so rescaling was only used when it was considered necessary to reduce overdispersion. To counter the near-non-convergence, the number of adaptive Gauss-Hermite quadrature points (nAGQ) was lowered to 0. This may slightly reduce the overall accuracy of the models, but it removed issues regarding non-convergence. We encountered further problems because some Invertebrate Measures were 0 within some transects, a value that could not be analysed by the models. To counter this, the value of 0.000001 was added to each of the Invertebrate Measure/per trap/per day classifications that held a 0. This is less than 0.01% of any of the mean values of these dependant variables. However, it did increases the overdispersion of the Slug Count, Arachnid Count, and Detritivore Count models. To counter this, these dependant variables were square rooted for the analysis which reduced overdispersion.

Four sets of models were constructed, each specific to one of four questions: First, to what extent does the release of pheasants impact the Invertebrate Measures and Habitat Scores within the release pen? Second, does the density at which the pheasants are released effect the Invertebrate Measures and Habitat Scores within the release pen? Third, to what extent does the percentage of released pheasants that were reared under Enhanced conditions effect the Invertebrate Measurements and Habitat Scores within the release pen? Fourth, to what extent do the Habitat Scores relate to Invertebrate Measures? This final question would help identify if changes to the Invertebrate Measures were driven directly by the release of pheasants or indirectly by the changes to habitat that the release might cause. We were unable to include all variables and their interactions in a single model (5 main effects + 20 two & three way interactions) because we had too few sample sites to permit this to be conducted robustly.

For our first set of models describing differences in Invertebrate Measures and Habitat Scores relating to pheasant releases, we included Invertebrate Measures and Habitat Scores as dependent variables, with a different one of the nine measures (Total Biomass, Total Count, Slug Count, Beetle Count, Arachnid Count, Detritivore Count, Bare Ground, Ground Vegetation, Shrubby Cover) in each model. We were specifically interested in differences between Interior and Exterior transects, so we considered interactions between transect location and other variables of interest. We expected Invertebrate Measures to vary across the three survey periods as invertebrate populations fluctuated naturally over time, so survey number was included in the three-way interaction. We wished to explore whether effects differed between years, so year was included in the three-way interaction. This is of particular interest due to climatic differences commonly occurring between years. During our study, 2017 was both a drier and hotter year overall compared to 2016 but was also predominantly wetter and slightly colder over the actual survey period (Table 4.8). This described model structure will now be referred to as the Base Model.

	Year	Jul	Aug	Sep	Oct	Nov	Annual
Rainfall (mm)	2016	35.1	64.8	59	28.3	95.6	781.4
	2017	79.9	68.2	84.5	46	54.9	741.2
Temp (°C)	2016	16.7	16.8	15.7	10.4	5.4	10.01
	2017	16.6	15.5	13.3	12.1	6.5	10.33

Table 4. 1 Average rainfall (mm) and temperature (°C) within the UK midlands for the survey period and average temperature and total rainfall for the entire year

For our second set of models, we were interested in the effect of Density on each of the Invertebrate Measures and Habitat Scores. As such, the Base Model structure was again used, but with the addition of the two-way interaction between Density and Survey Number to determine broad effects on invertebrates of changes in release pen stocking density over the three survey periods, and the three-way interaction between Trap Location, Survey Number and Density, to determine if the effects of Density from the two-way interaction differed between pen Interior and Exterior. This model structure is referred to as the Density Model.

For our third set of models, we were interested in the effect of the percentage of Enhanced birds released into the pen on each of the Invertebrate Measures and Habitat Scores. As such, the Base Model structure was again used, but with the addition of the two-way interaction between Percentage Enhanced and Survey Number to determine broad effects on invertebrates of changes in the percentages of Enhanced pheasants released over the three survey periods, and the three-way interaction between Trap Location, Survey Number and Percentage Enhanced, to determine if the effects of Percentage Enhanced from the two-way interaction differed between pen Interior and Exterior. This model structure is referred to as the Enhanced Model structure. For both the Density Models and the Enhanced Models, only the results from the coefficients involving Density and Percentage Enhanced were reported, as these were the focus of the models and constituted the only additions to the model structure beyond the Base Model.

For the fourth set of models, we were interested in the effect of each of the Habitat Scores on the Invertebrate Measures. This resulted in a model structure that had Invertebrate Measures as the Dependant Variable and each of the three Habitat Scores (Bare Ground, Vegetation 0-1m, or Vegetation 1-5m) as independent variables. We were also interested if any of the effects differed between Year, and so the two-way interaction between Year and each of the Habitat Scores was also added. Survey number was also included as an independent variable to account for overall changes in Invertebrate Measures between surveys. This model structure is referred to as the Invertebrate-Habitat Model. The definitions of all variables entered into all models can be found in Table 4.2 while the final model structures can be found in Table 4.3.

Separate analyses were conducted on each of these Invertebrate Measures, but as the individual Count variables are subdivision of Total Count, we recognise that the threshold for significance using P values should be reduced to account for multiple comparisons. However, as this was primarily an exploratory study, we retained the convention of significance being assumed when $P < 0.05$ while acknowledging that this increases the likelihood of Type 1 errors. For the Density Models, % changes in dependant variables were calculated by finding the difference in values when Density was increased from 0.2 to 0.3 pheasants per m^2. This value was selected as the mean stocking density of all pens was 0.258 pheasants per m^2. For the full range of stocking densities see Figure 4.1. Results within the Enhanced Model were calculated by finding the difference in dependant variable values when Enhanced Pheasant % was increased from 0% to 50%, which represented the median difference for our samples between pens with or without Enhanced birds.

All results presented in the final model tables are shown as % changes in their respective dependant variable. The results that were deemed significant ($P = <0.05$) were marked in **bold and underlined** in the results tables. Definitions of each table heading can be found in Table 4.4.

Variable Name	Variable Description
Survey Number	Whether the dependant variable was collected during Survey 1, 2, or 3.
Trap Location	Whether the dependant variable was collected from Interior or Exterior transects.
Percentage Enhanced	The percentage of Enhanced pheasants released into the pen.
Density	The density of pheasants released into the pen (pheasants/m^2 of pen area).
Year	The year of the survey, either 2016 (Year 1) or 2017 (Year 2)

Table 4. 2 Independent variables definitions used in the four model structures (excluding Habitat Scores for Invertebrate-Habitat Models).

Model Name	**Dependant Variable**	**Independent Variables**	**Random Effect**
Base Model	Invertebrate Measures and Habitat Scores	Survey Number	Pen Name
		Survey Number : Year	
		Survey Number : Trap Location : Year	
Density Model	Invertebrate Measures and Habitat Scores	Survey Number	Pen Name
		Survey Number : Year	
		Density : Survey Number	
		Survey Number : Trap Location : Year	
		Trap Location : Survey Number : Density	
Enhanced Model	Invertebrate Measures and Habitat Scores	Survey Number	Pen Name
		Survey Number : Year	
		Percentage Enhanced : Survey Number	
		Survey Number : Trap Location : Year	
		Trap Location : Survey Number : Percentage Enhanced	
Invert-Habitat Model	Invertebrate Measures	Survey Number	Pen Name
		% Bare Ground : Year	
		% Ground Vegetation : Year	
		% Shrubby Cover : Year	

Table 4. 3 GLMM model structures for Base, Density, Enhanced, and Invert-Habitat Models.

Contained within Model	Result column headings	Question being tested and result metrics
Base	Exterior Survey difference	Did the value assigned to the dependant variable on Survey 1 change significantly in Surveys 2 and 3 on the pen Exterior? Results in % change of dependant variable in Survey 2 or 3 when compared to Survey 1 on pen Exterior. Survey 1 left blank as it cannot be compared to itself.
Base	Between Year Exterior Survey Difference	Did the dependant variable for each Survey differ significantly in Year 2 when compared to the same Survey in Year 1 on pen Exterior? Results in % change of dependant variable between Exterior Surveys of Year 2 compared to the same Survey of Year 1.
Base	Interior Year 1	Did the Interior dependant variable differ significantly from Exterior for each Survey in Year 1? Results in % change in Interior dependant variable compared to Exterior for each Survey in Year 1.
Base	Interior Year 2	Did the Interior dependant variable differ significantly from Exterior for each Survey in Year 2? Results in % change in Interior dependant variable compared to Exterior for each Survey in Year 2.
Density	Exterior Density	Did increasing the Density of pheasants released significantly affect the dependant variable on pen Exteriors for each Survey. Results in % change of dependant variable on pen Exterior when pheasant per m^2 was increased by 0.1.
Density	Interior Density	Did increasing the Density of pheasants released significantly change the Interior dependant variable when compared to the Exterior. Results in % change of Interior dependant variable compared to Exterior when pheasants per m^2 was increased by 0.1.
Enhanced	Exterior Enhanced	Did increasing the percentage of Enhanced Pheasants released into in the release pen significantly change the Exterior dependant variable? Results in % change of Exterior dependant variable when Percentage Enhanced is increased from 0% to 50%.

Enhanced	Interior Enhanced	Did increasing the percentage of Enhanced pheasants released into the pen significantly change the Interior dependant variable when compared to the Exterior. Results in % change of Interior dependant variable compared to Exterior when Percentage Enhanced is increased from 0% to 50%.
Invertebrate-Habitat	% Bare Ground	What was the effect on the dependant variable of increasing the percentage of Bare Ground? Results in % change of dependant variable from an increase in Bare Ground of 10%.
Invertebrate -Habitat	% Ground Vegetation	What was the effect on the dependant variable of increasing the percentage of Ground Vegetation? Results in % change of dependant variable from an increase in Ground Vegetation of 10%.
Invertebrate –Habitat	% Shrubby Cover	What was the effect on the dependant variable of increasing the percentage of Shrubby Cover? Results in % change of dependant variable from an increase in Shrubby Cover of 10%.

Table 4. 4 Heading definitions for Base, Density, Enhanced, and Invertebrate-Habitat Models

4.3 Results

4.3.1 Coarse-scale seasonal and yearly changes in Invertebrate Measures (Base Model)

Invertebrate Measures were typically lower with successive Surveys within a year, although counts of Arachnids and Detritivores did not differ between Surveys 1, 2, and 3 (Table 4.5). All Invertebrate Measures were significantly lower in Year 2 when compared to the same Survey in Year 1 with the exception of Total Count and Total Biomass values in Survey 3 which did not differ and Arachnid Count and Detritivore Count which did not differ between Years across all Surveys (Table 4.5).

4.3.2 To what extent does the release of pheasants impact the Invertebrate Measures?

There were no differences in any Invertebrate Measures between Interior and Exterior transects during Survey 1 in either year (Table 4.5).

Some Invertebrate Measures differed between Interior and Exterior transects during Survey 2, but these were not consistent across years (Table 4.5). In Year 1, Interior Invertebrate Measures were lower than Exterior Measures for Total Biomass (-41.1% ±7.8, $P = 0.0009$, Fig 4.2), Slug Count (-36.1% ±8.73, $P = 0.0205$, Fig 4.4), and Detritivore Count (-49.2% ±9.33, $P = 0.0090$, Fig 4.5) in Survey 2. In Year 2, Interior Measures were lower than Exterior Measures for Arachnid Count (-66.3% ±7.16, $P = 0.0002$, Fig 4.4) in Survey 2.

Some Invertebrate Measures differed between Interior and Exterior transects during Survey 3, but these were not consistent across years (Table 4.5). In Year 1, there were no differences in any Invertebrate Measures between Interior and

Exterior transects in Survey 3 (Table 4.5). In Year 2, there were higher Total Biomass (51.7% ±19.3, P = 0.0082, Fig 4.2), Total Counts (65.8% ±19.2, P = 0.0002, Fig 4.3), Slug Counts (59.7% ±21.5, P = 0.0138, Fig 4.4), and Beetle Counts (72.0% ±23.8, P = 0.0020) in Interior compared to Exterior transects in Survey 3 (Table 4.5).

4.3.3 Does the density at which the pheasants are released affect the Invertebrate Measurements? (Density Model)

Our models revealed that increasing stocking density by 0.1 pheasants/m^2 was accompanied by a higher Slug Counts (23.8% ±17.2, P = 0.0010) and a lower Detritivore Count (-24.9% ±15.5, P = 0.0271) at Survey 1 across both pen Interior and Exterior transects equally (Table 4.6). The increased stocking density was also accompanied by lower Total Biomass from Interior transects during Survey 1 (-13.2% ±11.4, P = 0.0193) (Table 4.6). No other Invertebrate Measures differed significantly in any other Survey due to Density (Table 4.6).

4.3.4 Does the percentage of released pheasants that were reared under Enhanced conditions affect the Invertebrate Measurements? (Enhanced Model)

Our model revealed that an increase of Enhanced pheasant stocking from 0% to 50% was accompanied by increased Beetle Counts (43.3% ±22.4, P = 0.0484) from Interior compared to Exterior transects in Survey 1 (Table 4.7). No other Invertebrate Measures differed in any other Survey.

4.3.5 How do patterns of pheasant release affect Vegetation Coverage?

Within any one year, Exterior Habitat Scores did not change significantly between Surveys. Between years, Bare Ground and Shrubby Cover were higher both inside and outside release pens across all three surveys in Year 2 when compared to Year 1, whereas there were no differences between years in Ground Vegetation (Table 4.5).

There was a consistently greater extent of Bare Ground around Interior transects compared to Exterior ones in Survey 1 (303% ±55.2, $P < 0.0001$), Survey 2 (1160% ±172, $P < 0.0001$), and Survey 3 (1170% ±189, $P < 0.0001$) in Year 1 and Survey 1 (45.0% ±19.4, $P = 0.0173$), Survey 2 (129% ±30.7, $P < 0.0001$) and Survey 3 (153% ±33.9, $P < 0.0001$) in Year 2. (Table 4.5). There was consistently less Ground Vegetation surrounding Interior transects compared to Exterior ones recorded in Survey 2 (-75.2% ±3.22, $P < 0.0001$) and Survey 3 (-76.2% ±3.37, $P < 0.0001$) in Year 1 and Survey 2 (-70.0% ±3.82, $P < 0.0001$) and Survey 3 (-71.0% ±3.69, $P < 0.0001$) in Year 2, (Table 4.5). There was a greater area of Shrubby Cover around Interior transects compared to Exterior ones in Survey 1 (77.4 % ±20.8, P = <0. 0001), Survey 2 (77.4% ±20.8, $P < 0.0001$) and Survey 3 (86.6% ±23.4, $P < 0.0001$) in Year 1. However, this difference was absent during Survey 1 and 2 in Year 2 and the difference was then reversed, with a smaller area of Shrubby Cover around Interior transects compared to Exterior ones, during Surveys 3 (26.2% ±8.42, $P = 0.0096$) in Year 2 (Table 4.5).

Our model revealed that an increase in stocking density by 0.1 pheasants/m^2 was accompanied by a lower Exterior Shrubby Cover on Survey 1 (-12.1% ±10.3, $P = 0.0169$) and lower Interior Shrubby Cover in Survey 2 (-23.7% ±10.2, $P = 0.0191$) and Survey 3 (-25.8% ±11,4, $P = 0.0152$) (Table 4.6). Increasing the percentage of

Enhanced pheasants from 0% to 50% decreased Shrubby Cover in both Interior and Exterior transects in Survey 1 (-28.5% ±9.35, P = 0.0343), Survey 2 (-29.5% ±9.23, P = 0.0277), and Survey 3 (-33.3% ±9.17, P = 0.0132) (Table 4.7) but caused no significant differences between Interior and Exterior Habitat Scores in any Survey.

4.3.6 How does Vegetation Coverage relate to Invertebrate Measures?

Levels of ground coverage by vegetation were not consistently related to Invertebrate Measures. In Year 1, we found no relationship between Ground Vegetation coverage and any Invertebrate Measure, but in Year 2 our model revealed that a 10% increase in Ground Vegetation was accompanied by decreases in Total Biomass (-6.58% ±12.59, P = 0.0237) (Table 4.8). In neither Year 1 nor Year 2 was Bare Ground or Shrubby Cover coverage related to any Invertebrate Measure (Table 4.8).

Base Model		Exterior Survey difference			Between Year Exterior Survey Difference			Interior Year 1			Interior Year 2		
	Survey Number	1	2	3	1	2	3	1	2	3	1	2	3
Total Biomass	% Change	-	**-66.9**	**-90.6**	**-62.5**	**-60.1**	-9.36	-17.7	**-41.1**	-18.9	11.3	-4.29	**51.7**
	% Std Error	-	**4.29**	**1.34**	**4.77**	**5.07**	11.5	10.7	**7.63**	11.5	14.2	12.2	**19.3**
Total Count	% Change	-	**-49.6**	**-81.8**	**-45.3**	**-49.8**	24.1	-13.9	-23.8	6.12	14.7	5.02	**65.8**
	% Std Error	-	**5.95**	**2.34**	**6.34**	**5.81**	14.4	10.2	8.99	13.7	13.3	12.2	**19.2**
Sqrt Slug Count	% Change	-	**-54.8**	**-67.9**	**-70.3**	**-37.8**	**-33.7**	-4.2	**-36.1**	-13.2	6.55	-1.8	**59.7**
	% Std Error	-	**6.17**	**4.87**	**4**	**8.37**	**8.91**	13.1	**8.73**	13.2	14.3	13.2	**21.5**
Beetle Count	% Change	-	**-45.6**	**-82.3**	**-54**	**-49.8**	**57**	-14.6	-5.82	14.6	39.9	30.4	**72**
	% Std Error	-	**7.67**	**2.74**	**6.37**	**6.96**	**21.8**	12	13.3	17.8	19.4	18.1	**23.8**
Sqrt Arachnid Count	% Change	-	-20.7	-45.4	9.65	-0.854	-11.9	-11.8	-6.34	-9.72	-16	**-66.3**	-37.7
	% Std Error	-	17.1	13	23.3	21	18.7	19	20.2	21.6	17.8	**7.16**	13.2
Sqrt Detritivore Count	% Change	-	3.96	-22.1	50.8	7.15	-11.3	-15.7	**-49.2**	-2.94	-11.8	-30.9	-12.4
	% Std Error	-	19.1	15.9	27.3	19.4	16	15.5	**9.33**	19.8	16	12.5	15.8
Bare Ground	% Change	-	0	0.773	**438**	**564**	**522**	**303**	**1160**	**1170**	**45**	**129**	**153**
	% Std Error	-	13.7	15	**72.1**	**88.8**	**83.4**	**55.2**	**172**	**189**	**19.4**	**30.7**	**33.9**
Ground Veg	% Change	-	0	0.744	-3.1	-13.9	-6.25	-24.2	**-75.2**	**-76.2**	-23.2	**-70**	**-71**
	% Std Error	-	13	14.3	12.4	11	11.9	9.84	**3.22**	**3.37**	9.79	**3.82**	**3.69**
Shrubby	% Change	-	0	-0.31	**152**	**140**	**135**	**77.4**	**77.4**	**86.6**	-9.33	-20.5	**-26.2**
	% Std Error	-	11.7	12.5	**28.8**	**27.4**	**26.9**	**20.8**	**20.8**	**23.4**	10.4	9.07	**8.42**

Table 4. 5 Results of Base Models showing statistically significant (P < 0.05) changes in dependant variables in percentage increases or decreases across the various model criteria defined in table 4.3. Non-significant results (P > 0.05) are shown as *NS*. **Exterior Survey difference** = % change of dependant variable in Survey 2 or 3 when compared to Survey 1 on pen Exterior. **Between Year Exterior Survey Difference** = % change of dependant variable between a Survey of Year 2 compared to the same Survey of Year 1 on pen Exterior. **Interior Year 1** = % change in Interior dependant variable compared to Exterior for each Survey in Year 1. **Interior Year 2** = % change in Interior dependant variable compared to Exterior for each Survey in Year 2.

Density Model		Exterior Density			Interior Density		
	Survey Number	1	2	3	1	2	3
Total Biomass	% Change	10.2	-0.00491	2.57	**-14.1**	-3.23	6.17
	% Std Error	14.7	13.3	-85	**9.66**	7.58	12.1
Total Count	% Change	2.26	4.88	6.86	-4.91	-5.94	5.81
	% Std Error	12.4	12.7	-85.9	10	8.78	14.2
Sqrt Slug Count	% Change	**23.8**	0.572	2.56	-11.5	2.99	-0.0883
	% Std Error	**17.2**	14	-84.1	12.8	9.06	13.5
Beetle Count	% Change	1.31	8.79	7.19	-8.8	-11.4	8.22
	% Std Error	14.6	15.6	-83	11.4	12.6	18.3
Sqrt Arachnid Count	% Change	3.95	-0.833	5.96	0.921	1.15	6.32
	% Std Error	23.1	22.1	-73.8	19.6	21	22.8
Sqrt Detritivore Count	% Change	**-17.7**	-1.92	-5.55	12.2	7.03	3.79
	% Std Error	**15.6**	18.7	-80	18.1	10.3	21.2
Bare Ground	% Change	11.4	11.4	12.3	-57.3	-157	-186
	% Std Error	15.5	15.5	-83.1	52.6	163	176
Ground Veg	% Change	0.425	-3.95	-5.49	2.46	1.06	1.58
	% Std Error	13.5	12.9	-86.2	10.4	3.4	3.62
Shrubby	% Change	-12.1	-9.43	-8.58	-11.8	**-23.7**	**-25.8**
	% Std Error	10.4	10.7	-88.4	20.2	**19.4**	**21.7**

Table 4. 6 Results of Density Models showing statistically significant ($P < 0.05$) changes in dependant variables in percentage increases or decreases across the various model criteria defined in table 4.3. Non-significant results ($P > 0.05$) are shown as *NS*. **Exterior Density** = % change of dependant variable on pen Exterior when pheasant per m^2 was increased by 0.1. **Interior Density** = % change of Interior dependant variable compared to Exterior when pheasants per m^2 was increased by 0.1.

Enhanced Model		Exterior Enhanced			Interior Enhanced		
	Survey Number	1	2	3	1	2	3
Total Biomass	% Change	*-20.1*	*-9.65*	*-24.4*	16.2	13.2	12.6
	Std. error	*11.8*	*13.3*	*-88.1*	*13.2*	*9.38*	*13.6*
Total Count	% Change	*-16.9*	*21.6*	*-24.9*	*26.7*	*14.5*	*14.5*
	Std. error	*10.9*	*15.9*	*-89.5*	*12.9*	*10.7*	*15.6*
Sqrt Slug Count	% Change	*-22.6*	*-0.0894*	*-3.64*	*-8.16*	*14.5*	*2.86*
	Std. error	*11.6*	*15*	*-84.4*	*14*	*10.6*	*14.3*
Beetle Count	% Change	*-10.6*	*-0.143*	*-31.7*	**38**	*29.2*	*20.7*
	Std. error	*14*	*15.6*	*-88.5*	**15.8**	*16.6*	*20.3*
Sqrt Arachnid Count	% Change	*-9.26*	*8.38*	*-13*	*14.6*	*10.6*	*6.03*
	Std. error	*6.14*	*7.33*	*-93.7*	*6.72*	*6.15*	*7.46*
Sqrt Detritivore Count	% Change	*15.6*	*-3.99*	*40.6*	*19.2*	*28.1*	*30.9*
	Std. error	*25.1*	*20.8*	*-67.1*	*19*	*13.8*	*26.3*
Bare Ground	% Change	*13.6*	*30.5*	*22.5*	*190*	*-268*	*-233*
	Std. error	*17.3*	*19.8*	*-80.2*	*70.1*	*176*	*192*
Ground Veg	% Change	*12.3*	*4.72*	*-7.54*	*-24.5*	*-4.23*	*0.286*
	Std. error	*16.6*	*15.5*	*-85.5*	*9.77*	*3.42*	*3.75*
Shrubby	% Change	**-28.5**	**-29.5**	**-33.3**	*-6.44*	*4.68*	*31.2*
	Std. error	**9.35**	**9.23**	**-90.8**	*22.9*	*23.5*	*27.3*

Table 4. 7 Results of Enhanced Models showing statistically significant ($P < 0.05$) changes in dependant variables in percentage increases or decreases across the various model criteria defined in table 4.3. Non-significant results ($P > 0.05$) are shown as *NS*. **Exterior Enhanced** = % change of Exterior dependant variable when Percentage Enhanced is increased from 0% to 50%. **Interior Enhanced** = % change of Interior dependant variable compared to Exterior when Percentage Enhanced is increased from 0% to 50%.

Invertebrate-Habitat Models		% Bare Ground		% Ground Veg		% Shrubby Cover	
Study Year	Survey Number	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
Total Biomass	% Change	*-5.5*	*-3.76*	*0.746*	**-6.58**	*-2.47*	*-3.42*
	Std Error	*18.9*	*19.8*	*19.6*	**19.2**	*20.8*	*21.9*
Total Count	% Change	*-0.194*	*0.898*	*1.98*	*-3.41*	*-3*	*-1.93*
	Std Error	*18.5*	*19.2*	*18.4*	*18.3*	*19.2*	*20.6*
Insect Count	% Change	*0.0313*	*-1.68*	*3.59*	*-3.88*	*-2.36*	*-2.65*
	Std Error	*19*	*19.5*	*19.2*	*19*	*20*	*21.4*
Slug Count	% Change	*0.584*	*2.97*	*1.61*	*-3.29*	*-2.97*	*-3.65*
	Std Error	*22.1*	*23.3*	*21.7*	*21.8*	*22.7*	*24*
Beetle Count	% Change	*2.65*	*-0.0383*	*2.17*	*0.66*	*0.665*	*-0.507*
	Std Error	*29.8*	*30.2*	*28.8*	*30.3*	*31.4*	*33.2*
Arachnid Count	% Change	*2.65*	*-0.0383*	*2.17*	*0.66*	*0.665*	*-0.507*
	Std Error	*29.8*	*30.2*	*28.8*	*30.3*	*31.4*	*33.2*
Detritivore Count	% Change	*-6.26*	*-2.2*	*-4.12*	*-7.04*	*-2.34*	*3.13*
	Std Error	*24.7*	*26.9*	*24.6*	*25.5*	*27.7*	*31.3*

Table 4. 8 Results of Invert-Habitat Models showing statistically significant ($P < 0.05$) changes in dependant variables in percentage increases or decreases across the various model criteria defined in table 4.3. Non-significant results ($P > 0.05$) are shown as *NS*. **% Bare Ground** = % change of dependant variable from an increase in Bare Ground of 10%. **% Ground Vegetation** = % change of dependant variable from an increase in Ground Vegetation of 10%. **% Shrubby Cover** = % change of dependant variable from an increase in Shrubby Cover of 10%.

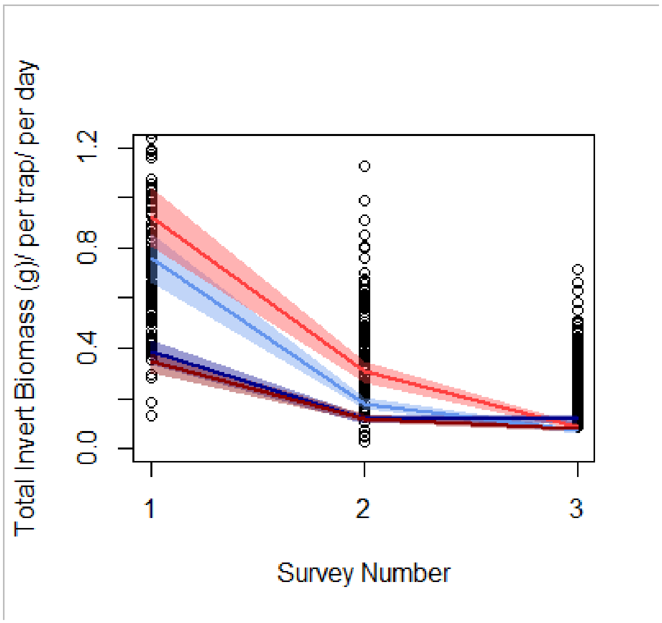

Figure 4.2 Release pen Interior and Exterior Total Invertebrate Biomass changes between Surveys across Years 1 and 2. Light Blue = Year 1 Interior, Light Red = Year 1 Exterior, Dark Blue = Year 2 Interior, Dark Red = Year 2 Exterior.

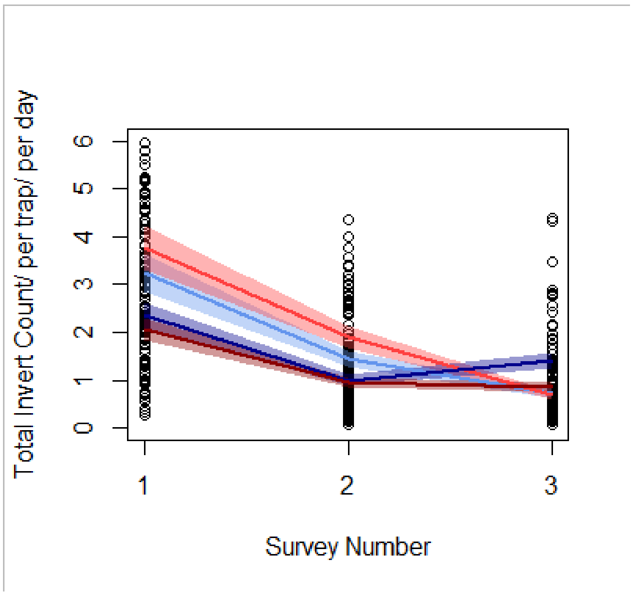

Figure 4.3 Release pen Interior and Exterior Total Invertebrate Count changes between Surveys across Years 1 and 2. Light Blue = Year 1 Interior, Light Red = Year 1 Exterior, Dark Blue = Year 2 Interior, Dark Red = Year 2 Exterior.

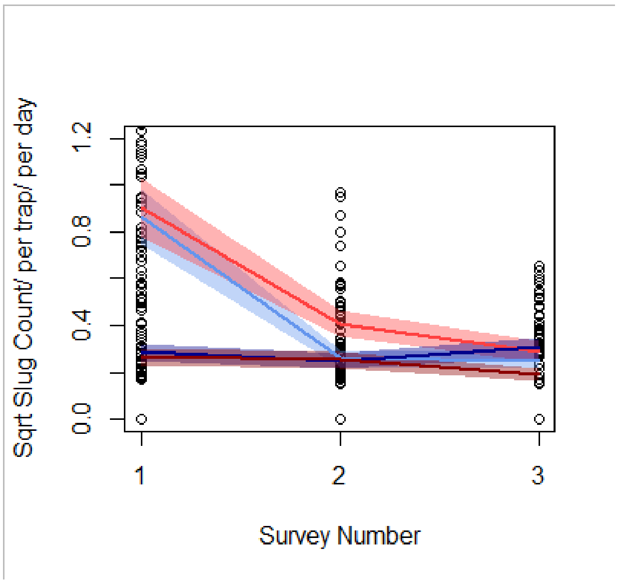

Figure 4.4 Release pen Interior and Exterior Slug Count changes between Surveys across Years 1 and 2. Light Blue = Year 1 Interior, Light Red = Year 1 Exterior, Dark Blue = Year 2 Interior, Dark Red = Year 2 Exterior.

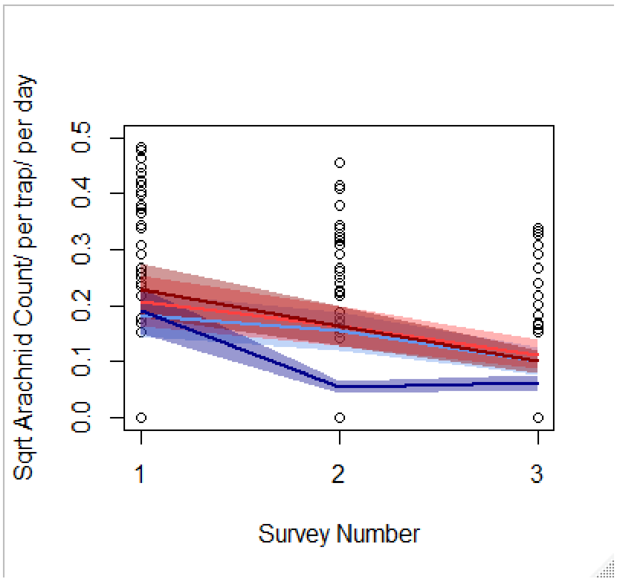

Figure 4.5 Release pen Interior and Exterior Arachnid Count changes between Surveys across Years 1 and 2. Light Blue = Year 1 Interior, Light Red = Year 1 Exterior, Dark Blue = Year 2 Interior, Dark Red = Year 2 Exterior.

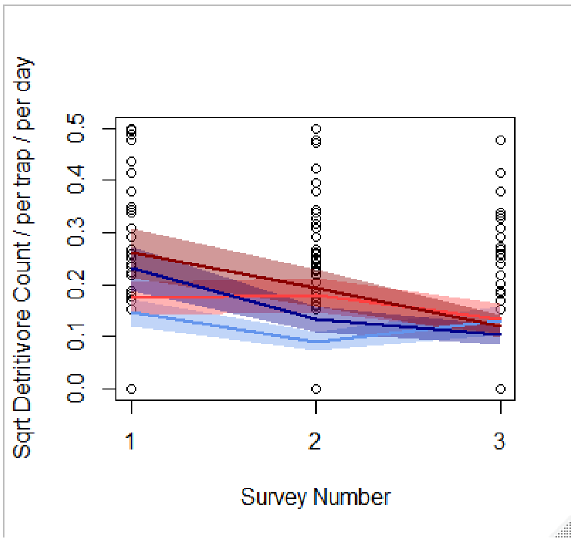

Figure 4.6 Release pen Interior and Exterior square rooted Detritivore Count changes between Surveys across Years 1 and 2. Light Blue = Year 1 Interior, Light Red = Year 1 Exterior, Dark Blue = Year 2 Interior, Dark Red = Year 2 Exterior.

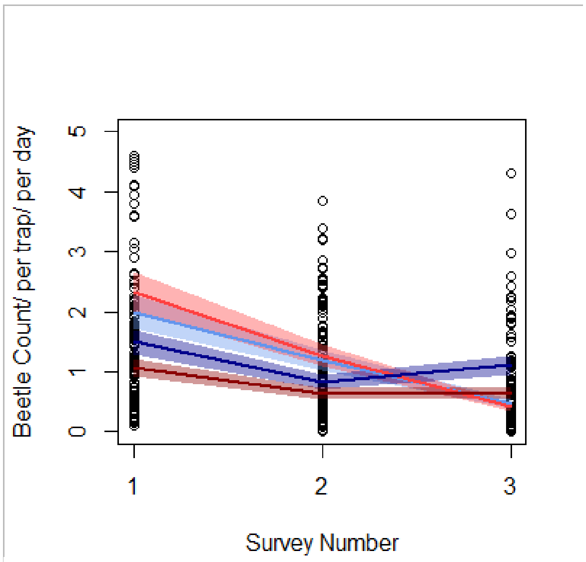

Figure 4.7 Release pen Interior and Exterior square rooted Beetle Count changes between Surveys across Years 1 and 2. Light Blue = Year 1 Interior, Light Red = Year 1 Exterior, Dark Blue = Year 2 Interior, Dark Red = Year 2 Exterior.

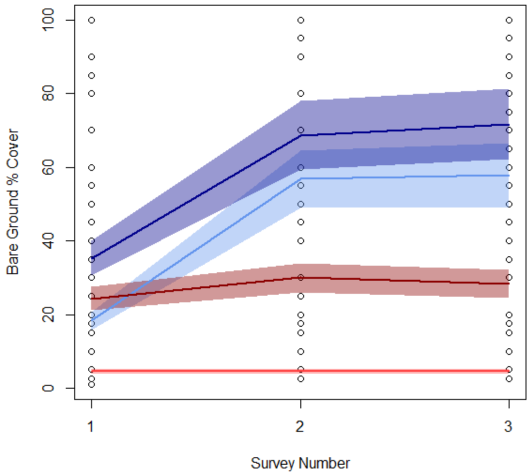

Figure 4.8 Release pen Interior and Exterior Bare Ground % Cover changes between Surveys across Years 1 and 2. Light Blue = Year 1 Interior. Light Red = Year 1 Exterior. Dark Blue = Year 2 Interior. Dark Red = Year 2 Exterior.

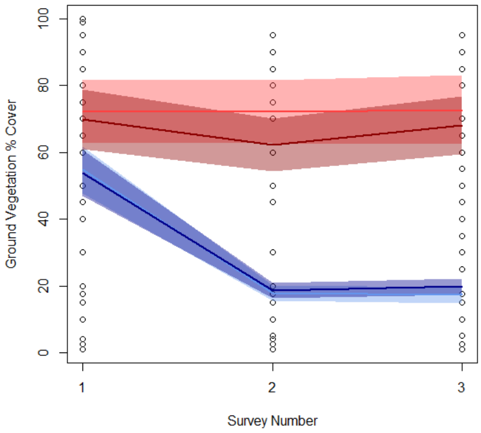

Figure 4.9 Release pen Interior and Exterior Ground Vegetation % Cover changes between Surveys across Years 1 and 2. Light Blue = Year 1 Interior, Light Red = Year 1 Exterior, Dark Blue = Year 2 Interior, Dark Red = Year 2 Exterior.

4.4. Discussion

The effects on invertebrates of releasing pheasants into woodland pens were inconsistent, varying within and between years, and different according to the taxonomic grouping considered. Generally, we detected no differences between Invertebrate Measures made on Interior and Exterior transects during Survey 1, before pheasants had been released into the pen. This suggests that there were no inherent differences in invertebrates between areas inside and outside the release pens in the absence of pheasants. When pheasants were inhabiting the pens, during Survey 2, we detected some lower Invertebrate Measures recorded on Interior transects compared to Exterior ones. These were more evident during 2016 with differences between transect locations in Total Biomass, Slug Count, and Detritivore Count. In 2017, we only detected differences in Arachnid Count at this time. As the released pheasants spread away from the pens and out into the surrounding landscape, during Survey 3, we found some evidence that Invertebrate Measures inside the pen were now higher than those outside the pen. These differences were not evident in 2016, but in 2017 we found that Total Biomass, Total Count, Slug Count, and Beetle Count were higher on Interior transects compared to Exterior ones. Increasing pen stocking Density only affected Invertebrate Measures prior to release, lowering Interior Total Biomass and Interior and Exterior Detritivore Counts and causing higher Interior and Exterior Slug Counts. Increased stocking of Enhanced pheasants caused higher Beetle Counts and lower Shrubby Cover prior to release.

Invertebrate Measures, apart from Arachnid and Detritivore Counts, declined both inside and outside the release pen over the period of our surveys within each year, with the largest declines typically occurring between Surveys 1 and 2. This period corresponds to the introduction of pheasants into the pen. These absolute declines, regardless of transect location, could indicate that the release of pheasants has immediate, widespread effects on invertebrate populations in woods where pheasants are released. However, pheasants typically do not leave their release pens during these first few weeks (Hill and Robertson, 1988b), so we doubt whether these absolute declines are due to direct predation. Instead, declines outside the pen may occur because predation on invertebrates within the pen produces vacant niches that draw invertebrates in from outside and the pen may act as a population sink, so reducing their abundance outside. Alternatively, and we believe far more likely, absolute declines in Invertebrate Measures reflect non-pheasant related declines in populations as the year progresses (Wolda, 1988), with Survey 1 typically conducted in July-August and Surveys 2 and 3 typically occurring between September and November. Carabids, which constituted 92.3% of the total Beetle Count, are most active in late summer, with some species being 3 times as active then than in winter (Cartellieri and Lövei, 2003), and predatory arthropod populations have been shown to peak in June/July (Kovanci, Kovanci and Gencer, 2007). These seasonal differences would seem to match the patterns shown here. Arachnids and detritivores were consistent between surveys, but this may have been due to low count values making changes harder to detect. This may also explain why Arachnid and Detritivore Counts were also both the only Invertebrate Measures that were not significantly lower in 2017 than 2016 across the entire survey period. With the exception of Arachnid and Detritivore Counts, all 2017 Invertebrate Measures were significantly lower than those made in 2016 across the entire survey period. Similar differences between years were found for Habitat Scores, with higher Exterior Bare

Ground and Shrubby Cover in 2017, putting those habitat percentage covers closer to those levels found within the pen prior to release. We suspect that one explanation for these between-year differences is climatic variation, with 2017 being both a drier and hotter year overall compared to 2016 but also being predominantly wetter and slightly colder over the actual survey period (Met Office, 2019). Wetter and colder weather may have reduced invertebrate movement and decreased the likelihood of them falling into the pitfall traps (Saska *et al.*, 2013). Conversely, changes in climate may have made food less available and reduced the carrying capacity of the woodlands to support as many invertebrates (Dempster and Pollard, 1981), reducing their overall abundance. The different effect that we found between years may indicate that the effects of pheasant releases on both invertebrates and habitat can be mediated by additional natural processes such as changes in annual temperature and rainfall. Possible mechanisms for this could be increased bare ground and reduced invertebrate abundance shifting pheasant foraging strategies or reduced invertebrate movement making them less vulnerable to predation.

The Interior transects of pens had consistently more Bare Ground compared to neighbouring Exterior transects during all three Surveys in both years. This difference was matched by lower coverage by Ground Vegetation recorded during Surveys 2 and 3. These results suggest that either scratching by pheasants during foraging (Hill and Robertson, 1988) or simple trampling may remove ground vegetation within release pens. Shrubby Cover, being raised off the ground, is less likely to be directly affected by these behaviours, and this may explain why we see no post-release decreases in measures of this vegetation type in 2016, but in 2017, the release of pheasants caused Interior Shrubby Cover to decrease in Surveys 2 &

3. This effect could have been exaggerated by the wetter and colder weather during the release period in 2017 causing pheasants to spend more time roosting off the ground in Shrubby Cover to remain dry, resulting in damage to Shrubby Cover foliage.

An indirect effect of pheasant releases is changes in habitat structure (Sage, Ludolf and Robertson, 2005; Sage *et al.*, 2009), and although we also detected changes in habitats following release of pheasants, we found very limited evidence that this explained differences in Invertebrate Measures. No direct relationship was found between either Shrubby Cover or Bare Ground and any Invertebrate Measures. The only evidence that we found of habitat cover directly relating to Invertebrate Measures was for Ground Vegetation, with increased Ground Vegetation being associated with lower Total Biomass in 2017, but this relationship was inconsistent and not observed in 2016. This association with lower Total Biomass but not lower Total Count implies that increased Ground Vegetation is negatively affecting larger invertebrates. This could be because movement through a denser ground layer may be harder for larger invertebrates which, in a year where food items may be less available due to colder and wetter weather and greater distance must be travelled between foraging patches due to increased bare ground (Hassell and Southwood, 1978), would put larger invertebrates at a disadvantage to smaller more mobile invertebrates.

There were no differences between Invertebrate Measures inside and outside of release pens prior to release when not accounting for stocking density, indicating an absence of chronic between-year effects on invertebrates despite chronic effects being evident for vegetation cover. Pressland (2009) showed that pheasant releases do exert a chronic effect on invertebrate biomass, reducing it at the woodland scale, with evidence of lower levels of biomass prior to release. Although we did not study non-release woodlands, our study does show that this effect of reduced biomass from the presence of pheasants does not appear to be higher in general within the release pens. However, at pens where the density at which pheasants have been released in previous years was high, we detected lower Total Biomass within the release pen prior to release. This will be further discussed later with the other effects of density.

The reduced Total Biomass, Slug Count, and Detritivore Count within the pens 4 weeks post-release in 2016 show that pheasants can have a direct negative effect on invertebrates. The cause is likely direct predation, as adult pheasants will readily consume arthropods, molluscs, and even small vertebrates (Hill and Robertson, 1988b), and so despite pheasant diet having shifted away from being primarily base on invertebrates to grains and shoots by the time of release (Hill, 1985), they are likely still predating enough invertebrates to have a detrimental impact at a population level. The lower Interior Total Biomass but not Total Count seen in Survey 2 also implies that either the presence of pheasants is making the invertebrate population as a whole reduce in weight, or far more likely, that the largest individuals are being most negatively affected. In addition to larger invertebrates offering greater nutritional value to pheasants, less ground vegetation would make larger invertebrates more visually conspicuous and put them at higher risk of predation (Berger, Walters and Gotthard, 2006). Additionally, Neumann et al

(2015) found that higher pheasant densities reduced larger carabid populations within release pens in spring, indicating that larger invertebrates are more negatively affected by pheasant releases at both the long and short term.

These immediate effects of pheasant release on invertebrates shown in 2016 were not repeated in 2017, but instead, there were lower Interior Arachnid Counts, possibly caused by the combination of increased Interior Bare Ground with the now reduced prey numbers reducing the success of trap/ambush predator strategies of an arachnid population that itself had not declined on the pen Exterior (Nyffeler, 1996; Jocque *et al.*, 2011). Interior Total Biomass and Slug Count may not have been detected as being lower post-release in 2017 despite their being so in 2016 because the reduced values of these Invertebrate Measures decreased our ability to detect change, with Survey 2 Total Biomass and Slug Count being 60.1% and 37.8% lower respectively in 2017 than in 2016. This, however, does not explain the lack of an effect seen in Detritivore Count in Survey 2 of 2017, as Detritivore Count did not decline between years.

By 9 weeks post-release in 2016, the differences seen 4 weeks post-release had disappeared, despite the changes to habitat still being present. It is between Surveys 2 and 3 that the pheasants disperse from the release pens and out into the wider habitat, substantially reducing their concentrations within the pen. As such, the removal of these differences between the surveys further strengthens the argument that they were caused directly by the presence of pheasants. The fact that Total Biomass, Slug Count, and Detritivore Count now did not differ at all could be caused by one of or a combination of either the Invertebrate Measures within the pen recovering in the absence of pheasants, or those Invertebrate Measures outside the pen now becoming lower due to pheasants now being present as they disperse from the pen. Total Biomass and Total, Slug, and Beetle Counts were all significantly higher within the release pens in Survey 3 of 2017 whereas in 2016 there were no significant differences between any Invertebrate Measures collected from pen Interior and Exterior transects at this time. A possible explanation for this would be that food availability was the cause of the overall population declines in 2017. If the trampling of plant material and the accumulation of faeces within the release pen caused by pheasants (Sage, Ludolf and Robertson, 2005) increased the amount of food available to invertebrates, then it may explain why a greater number were present inside the pen once the predation pressure of pheasants had been lowered due to them largely dispersing away. This effect may not have been seen in 2016 if food sources were more widely available outside of the release pen. Detritivore Count was not higher on pen Interior in Survey 3 of 2017, but the freshly trampled plant matter would likely still be too fresh and a less favourable food source for woodlice (Zimmer, 1997), which constituted 71.08% of the mean Detritivore Count in this study. If more invertebrates had been drawn to pen Interiors in 2017 after release, it may have also played a part in there no longer being significant differences between Interior and Exterior Invertebrate Measures in Survey 2 of 2017.

We found little evidence that, within the range that we sampled, the density at which pheasants were stocked had any immediate effect on Invertebrate Measures, with stocking density failing to explain any of the additional variance in differences between Interior and Exterior transects recorded during Surveys 2 or 3. However, we did detect some evidence of a chronic effect of stocking density with lower Interior transect Total Biomass recorded at pens where a high density of pheasants was later released. Clearly, this couldn’t be an anticipatory effect, but instead, because stocking densities at pens are often consistent from year to year as game keepers simply repeat what they have done previously, we suspect that there may be cumulative consequences of repeated high density releases. Neumann et al (2015) found that spring populations of larger carabid beetles were lower inside release pens that had previously released pheasants at high densities, but our findings imply that a history of higher density releases lowers the quantity of all larger invertebrates prior to release, not just carabids, as shown by the decline in Total Biomass without a corresponding decline in Total Count, suggesting that the mean individual size is smaller. As this is only apparent before release, this change is likely due to the longer-term effects of pheasant releases, such as degradation of habitat (Sage, Ludolf and Robertson, 2005; Capstick, Sage and Hoodless, 2019), as opposed to direct predation. We also found that increased stocking density led to higher Slug Counts and lower Detritivore Counts prior to release that did not differ significantly between Interior and Exterior transects, though these effects were only present in Survey 1. This lower Detritivore Count both inside and outside of the release pen prior to release does not support findings by Neuman et al (2015) who found that spring populations of woodlice were higher within release pens that released pheasants at higher densities. We are unable to demonstrate a mechanism that might be causing this reduction in Detritivore Count (which was primarily woodlice) both inside and outside of the pen prior to release. Higher release densities in previous years causing higher Slug Counts both inside and outside of the pen prior to subsequent releases is also an unusual result considering that the release of pheasants, at least when slugs were more abundant in 2016, reduced slug abundance within the release pen. This implies that over the short term, pheasants negatively affect slug populations, but over the long term, increased pheasant densities may increase slug populations within and immediately around the release pens before pheasants are once again released. This may be because increased pheasant release densities has been shown to increase grasses, annuals, and perennials associated with fertile or disturbed soils within release pens (Sage, Ludolf and Robertson, 2005), and it is likely that increased pheasant densities also increase the number of these plants in the areas immediately around the release pens in the same manner that they do to the hedgerows near to pens (Sage *et al.*, 2009). Such high-nutrient and disturbance-tolerant species would grow faster than the shade-tolerant and low-nutrient specialist species of flora found within most woodlands (Aerts, 1999), and as such could provide more readily available sources of food for slug populations. Stocking density also had some effects on habitat composition, specifically, increased density leading to lower Shrubby Cover in Interior transects in Surveys 2 and 3. This is likely due to a higher number of pheasants using the Shrubby Cover as roosting, resulting in greater deterioration. The absence of this difference in Survey 1 indicates that the level of deterioration is recoverable between years. The densities of pheasant releases in this study were all relatively high, with only 3 of the 65 releases having stocking densities lower than the 0.07 birds/m^2 700 recommended by the GWCT (Sage and Swan, 2003), and only 9 pen densities being lower than the 0.1 birds/m^2 required to reduce shifts in floral compositions and long term habitat degradation (Sage, Ludolf and Robertson, 2005; Capstick, Sage and Hoodless, 2019). Therefore, it is possible that we encountered a ceiling effect where maximal degradation occurred at (almost) all pens because there were very few pens where release densities were low enough to exert little pressure. This may indicate why we did not find expected significant relationships between higher stocking density and habitat degradation in the form of increased Bare Ground and reduced Ground Vegetation.

We found little evidence that the rearing methods used to produce the pheasants, specifically if they had prior experience of and hence greater competence at predating live invertebrates, immediately influenced any Invertebrate Measures. The two effects from increasing the percentage of Enhanced pheasants released that were deemed significant by our model were present prior to release during Survey 1, with the effect on Beetle Count no longer present post-release and the effect on Shrubby Cover changing little post-release. Enhanced birds were only released during the years of our study, in 2016 and 2017. Therefore the likelihood of them having exerted an effect in Survey 1, implying a chronic effect, was low. Instead we believe these effects are spurious with little biological relevance. Overall, we can conclude that the release of pheasants reared under Enhanced conditions in which they might be expected to become more efficient predators of live invertebrate prey (Whiteside, Sage and Madden, 2015) did not have immediate disproportionate negative effects on the invertebrate (or plant) community post-release when compared to pheasants reared under more conventional methods.

4.5 Conclusion

Young wild-reared pheasants are prolific insectivores (Hill, 1985), and so unnaturally large numbers of such individuals, such as occur in artificial release pens, may be expected to dramatically reduce invertebrate populations. However, we found little consistent evidence to suggest that this is a ubiquitous process, with those effects that we did detect often restricted to particular taxonomic groups in a particular year. We did not explicitly look at effects on particular species, but this would be informative, especially if releases occur in areas where species of conservation concern are found (Callegari, Bonham and Holloway, 2014). These differential effects on particular groupings could be due to direct predation, with pheasant targeting preferred, more available, or more conspicuous prey, rather than declines occurring because the local vegetation has been disturbed. More detailed study of pheasant foraging behaviour and prey choice could help explain why some invertebrate groups may be especially vulnerable to predation. We also found that relatively higher numbers of some taxonomic groups can be found within the release pens once pheasants have largely dispersed into the surrounding environment. This suggests that either pheasants actually make pens more attractive habitats to certain invertebrate groupings, or that the effects of depredation by pheasants increases once they leave the pen such that Exterior populations are more strongly affected by the released birds than Interior populations. We suspect that this second possibility is less likely for two reasons. First, as the year progresses, the proportion of invertebrate matter in pheasant diets decreases to <10% of their diet in October/November (Dalke, 1937; Lachlan and Bray, 1973, Hill and Robertson, 1988), suggesting that they may depredate insects less at his time. Second, as the birds disperse, they forage at a lower density (both because they occupy a far larger area of ground and because they die in fairly large numbers) (Madden, Hall and Whiteside, 2018), so their depredations (which are already at a lower level) are likely to be diluted. Instead, we suspect that the trampling, disturbance, and accumulation of faecal matter in pens may provide an attractive habitat for some particular invertebrate groups or make them more susceptible to trapping. Our study reveals that effects of pheasant release may be especially marked in particular years, perhaps when invertebrate populations are especially high. This may be because any differences are simply more detectable as margins of error decrease. Alternatively, differing conditions may alter pheasant foraging behaviour, perhaps offering them alternative non-invertebrate food such a fruits or nuts, or altering the movement patterns or conspicuousness of invertebrates. Our data were restricted to just two years, so we cannot differentiate these potential explanations. Extending such studies to more years could reveal when invertebrate populations may be expected to be especially vulnerable to pheasant releases. It could also permit a better understanding of accumulated or chronic effects of releases within an area where pheasant releases are repeated each year.

Chapter 5: How accurate is monitoring pheasant populations via differing patagial wing tags?

Abstract

Determining animal population numbers and age demographics are essential for planning effective management of harvested populations. Individuals may be marked either after capture or, if reared in captivity, before their release into the wild. They are then counted at harvest or later captures to determine harvest rates or population estimations. It is critical that marking techniques are robust and either reliable or have a well understood error pattern so that correction factors can be applied. Released pheasants are commonly marked using patagial tagging, offering a cheap and simple method of marking large numbers of pheasants. Typically, the Multi-Tag has been used by both researchers and shoots because it is cheap, easily used, and readily available. However, it may be susceptible to damage or loss. We compared the durability of Multi-Tags against the more durable Plastags, with one of each placed in the wings of 2500 released pheasants, of which 866 were later shot or captured. We calculate that average underestimations of tag counts for the shooting season following tagging were 14.7% for fully intact Multi-Tags, 5.2% for intact Multi-Tags and Multi-Tag nubs, and 1.3% for Plastags. This may encourage shoot owners using Multi-Tags to either release more birds than necessary or spend resources tailoring their management to accommodate more immigrant or wild pheasants. Rates of Multi-Tag losses between years were too high for the reliable application of a correction factor. Consequently, we suggest that Plastags, rather than Multi-Tags, should be used to study year-to-year survival of gamebirds.

5.1 Introduction

In order to effectively manage land for gamebirds, data is required on lifespan, habitat use, and most importantly, population sizes (Tapper, 1988; Aebischer and Ewald, 2004). This is of particular relevance for species that are released for hunting, such as pheasants (*Phasianus colchicus*), where the collection of more data can allow game managers to adjust the efficiency of their management strategies, permitting them to reduce release sizes but maintain harvests (Robertson and Rosenberg, 1988; Turner, 2007). On pheasant shoots, such careful refinement of release sizes can limit the negative environmental, ethical, and economic effects of large scale releases (Sage, Ludolf and Robertson, 2005; Sage *et al.*, 2009; Capstick, Sage and Hoodless, 2019).

Several types of information about the harvested population that could inform future management decisions can be collected. Most simply, the proportion of the population that has been harvested can be calculated (Robertson and Rosenberg, 1988; Robertson *et al.*, 2017). For wild populations, collecting this information involves conducting surveys before harvest begins, noting numbers, sex, age and (typically breeding) location of individuals of the focal species, and then comparing the numbers and other attributes of those harvested with the original population estimates (Robinson *et al.*, 2008). For systems that release game to be harvested later, such as pheasant and red-legged partridges (*Alectoris rufa*) shot in the UK or salmonids released for angling (Tapper 1999), individuals can be accurately counted, aged, sexed, and marked upon release, depending on the marking method. These marks can then be retrieved at harvest. More detailed conclusions can be drawn from interpretations of these data. First, the overall efficiency of the harvest can be determined (Turner, 2007), providing information on how many animals should be released in subsequent years to reach specific harvest quotas. Second, marking can inform managers as to the effectiveness of different management strategies, mapping populations declines and highlighting possible causes (Peek, Lovaas and Rouse, 1967). Detailed management decisions may depend on information such as the age (Draycott, Pock and Carroll, 2002) or sex (Leif, 2005) structure of a population, or understanding of patterns of movement prior to and during harvest (Guthery, 1983). Third, marking data can allow managers to identify release areas that are not productive, allowing them to improve or remove them from future releases and further improve efficiency. Fourth, by considering the numbers and age/sex structure of unmarked individuals, the game manager of a release-based harvest system may gain insights into the health of the wild population based on the contribution it make to the harvest (Barnett-Johnson, 2007). Such data can inform the game manager about consequent management decisions about the scale, composition, and locations for future releases.

However, the utility of such data is entirely dependent on the reliability of the marking system. Unreliable marking can cause underestimations of harvest efficiency and lead to larger releases; can cause the continued use of poorly performing releases sites increasing ‘wastage’ in released animals; reduce the accuracy of information on immigration and dispersal; and inflate estimates of the wild animals currently within the landscape. Because of these reasons it is essential that methods of marking released animals are either reliable or the rate of errors are known so that correction factors can be applied.

Pheasants are commonly artificially reared and released in the UK to facilitate game shooting. This activity is practiced across the lowland UK and involves the annual release of 39-57 million birds (Aebischer, 2019). Consequently, accurate information about populations and harvest outcomes are critical to good management of this resource. A range of methods exist for monitoring gamebird populations sizes. At the most basic, population estimates can be obtained for free-living birds by direct counts (Potts, 1986; Tapper, 1988; Walsh *et al.*, 2004) or counting vocalisations (Rice, 2003), but this often requires experienced workers and extensive time to collect sufficient data (Carney and Petrides, 1957). Such population counts can then be compared to harvest records, but this may be too simplistic for detailed analysis and effective gamebird management, as it gives no information on the age or provenance of the birds. Much more detailed information may arise from the deployment of radio-tags on the birds and monitoring them in real time. For pheasants, this has been used to provide good data on movement and survival both on chicks (Hill, 1985) and adults (Whiteside and Guthery, 1944; Sage *et al.*, 2018). However, this method requires large amounts of effort in capturing, applying radio tags, and then manually monitoring the birds while also having significant costs; therefore few individuals can be followed. An alternative method that balances costs, numbers of individuals considered and data richness, and is suitable for populations that are reared and then released, is to mark individuals on release with some form of passive tag that can be retrieved at harvest.

Tags can convey information about the origin or release point of the bird and deployment records which describe the released population can be compared against recovered tags from the harvested population. Marking gamebirds for visual identification for research has been used since 1956 (Ash, 1956), with examples of commonly used current methods being neck bands (Gerald A . Bartelt and Donald H ., 1980) and wing tagging (Whiteside, Sage and Madden, 2016). Patagial tags, with large numbered markers for identification at distance, allow for small scale studies of gamebird group dynamics, mortality, and dispersal (Whiteside, Sage and Madden, 2015; Whiteside, Langley and Madden, 2016). However, using tags that are visible from a distance best serves studies into individual birds as opposed to populations as a whole, and although methods such as coloured leg banding can have some use for large scale releases, they also require greater time, effort, and cost to deploy (Gullion, Eng and Kupa, 1962). Small tags that identify individuals and their origins, but don’t facilitate visual identification at a distance, allow gamebirds to be identified after being shot or recaptured and can result in extensive population level datasets. Passive Integrated Transponders (PIT) tags can work very effectively in this respect and have shown low levels of deterioration after harvests (via shooting) (Carver, Vincent A, Burger, Loren W., Brennan, 1999). However, their main drawback is cost (Jamison *et al.*, 2000), with current prices of PIT tags at $3.00 each (Oregon RFID, 2018). For gamebirds that are released by the (tens of) thousands, such costs are excessive. A more cost-effective solution is the use of simple coloured and dated patagial tags which can be easily fitted to young or mature gamebirds. The application of patagial tags is far swifter than other tagging method, with a pair of experience taggers able to tag up to 12 birds per minute depending on the type of tag used (my own research). The tags can be applied to 6-8 week old pheasant poults immediately prior to their delivery to shoots, and there is little issue of the tag causing harm to the bird as it grows, which has been found for some bird species for similarly purposed leg bands (Berggren and Low, 2005; Trefry, Diamond and Jesson, 2012). Such patagial tags can be metal or plastic and can convey additional information via number or date stamping or colour coding to facilitate individual ID, year of release, or location of release. Tags can easily be counted by non-specialists inspecting shot pheasants and, with coordinated tagging operations, tags being detected on neighbouring shoots can reveal patterns of dispersal (Whiteside, Sage and Madden, 2015). Although the application of patagial tags has been shown to increase the rate of nest desertions in breeding Least Terns (*Sternula antillarum*) in Texas (Brubeck, Thompson and Slack, 1981), the rate of nest failure in seabirds (Trefry, Diamond and Jesson, 2012), and potentially increasing the rate of predation of hen harriers (*Circus cyaneus*) (Zuberogoitia *et al.*, 2012), there have been no significant ill effects recorded in studies where pheasants have received simple coloured or dated patagial tags (Sage, Putaala and Woodburn, 1996; Sage *et al.*, 2003; Turner, 2007).

The Multi-Tag/Quick-Tag (MT) is the design most commonly used for mass tagging of pheasants prior to release (Fig 5.1). These simple, lightweight plastic tags are 33mm in length and are cheap (~£0.0325 per tag, Perdix Wildlife Supplies, Warwickshire, UK, 2018). They have been used extensively in the Game and Wildlife Conservation Trust's National Game Marking Scheme (NGMS) (Game and Wildlife Conservation Trust, 2019). This project has been running since 2009 and supplies MTs to shoots and game rearer so that they can record the number of tagged birds released from each individual pen within each shoot-day's harvest. This allows for the collection of harvest at a national level, as well as enabling participating shoots themselves to analyse their management practices. MTs can carry additional information in the form of numbers written on a large plastic tail or use of different colours perhaps conveying the year or point of release. This permits the recording of year-to-year survival or patterns of dispersal from release point to recovery. However, initial research into Enhanced Rearing techniques tested during this thesis found that the rate of deterioration of the MTs over time appeared markedly high. Deterioration either came from the MTs falling off completely or through damage resulting in the detachment of the plastic tail leaving just the small coloured plastic bars (nubs) within the wing. This loss of (a large and conspicuous) part of the tag makes it much harder to locate, increasing the likelihood of human error while recording tag returns and, because the tail was printed with the date of release, it prevents acquisition of year-to-year survival records.

We were aware of an alternative patagial tag, the Plastag (Plastag B, available from Roxan Ltd, Selkirk, UK, 2018). This tag is significantly more durable than the MT and attaches to the bird via a pin that pierces the patagial skin and binds the two ends of the tag together. It is 56mm in length before the pin seals the ends together. Once sealed it is 28mm (Fig. 5.1). However, it is also more than three times as expensive than MTs, with the price for each tag at £0.103 (Roxan International, 2018).

This study explores if the use of this more durable patagial tag can be used to calculate the rate of deterioration over time for the MTs so that a correction factor can be added to datasets created using MTs, increasing the accuracy of both research and information collected by game managers which could lead to more reliable research outcomes and more effective gamebird management. Additionally, it also seeks to assess the overall viability of MTs for long term data collection and if the Plastag would be a preferable alternative for future studies.

5.2 Methods

5.2.1 Tag Application

We released 2,500 male pheasants at Loddington Estate, Leicestershire in 2017. Birds were purchased from a commercial game rearer and delivered to Loddington when 7 weeks old. All pheasants were tagged on delivery with a Multi-Tag (MT) in one wing and a Plastag in the other, with the placement side randomised. Loddington is one of the GWCT's research sites and releases only male birds as part of their release strategy, tagging them each year to gather data on their release and harvest rates.

Multi-Tags were applied using a tagging gun (Available from: Perdix Wildlife Supplies, Warwickshire, UK, 2018) by piercing the patagial skin above the muscle tissue to inject the lower bar of the tag through the patagial skin. The bar is then released from the needle and is unable to pass back through the injection hole. This leaves the lower bar beneath the wing and the upper bar with the date-flap protruding vertically above the wing. Depending on the skill of the worker and the movement of the bird, MT application took ~5-10 seconds per tag, but this could be highly variable as the tagging gun commonly jammed, substantially delaying tag deployment.

Plastags were applied using an applicator clamp (available from Roxan Ltd, Selkirk, UK, 2018) on the opposite wing to the MT. The clamp ensured that the tag's spike pierced the patagial skin and locked the upper and lower sides of the tag in place. Plastag application took ~10-15 seconds per tag with no instances of delays due to jamming. Tags were applied by 4 workers with experience in various tag applications ranging from moderate to very experienced. All tags were checked to ensure that each was securely in place after application.

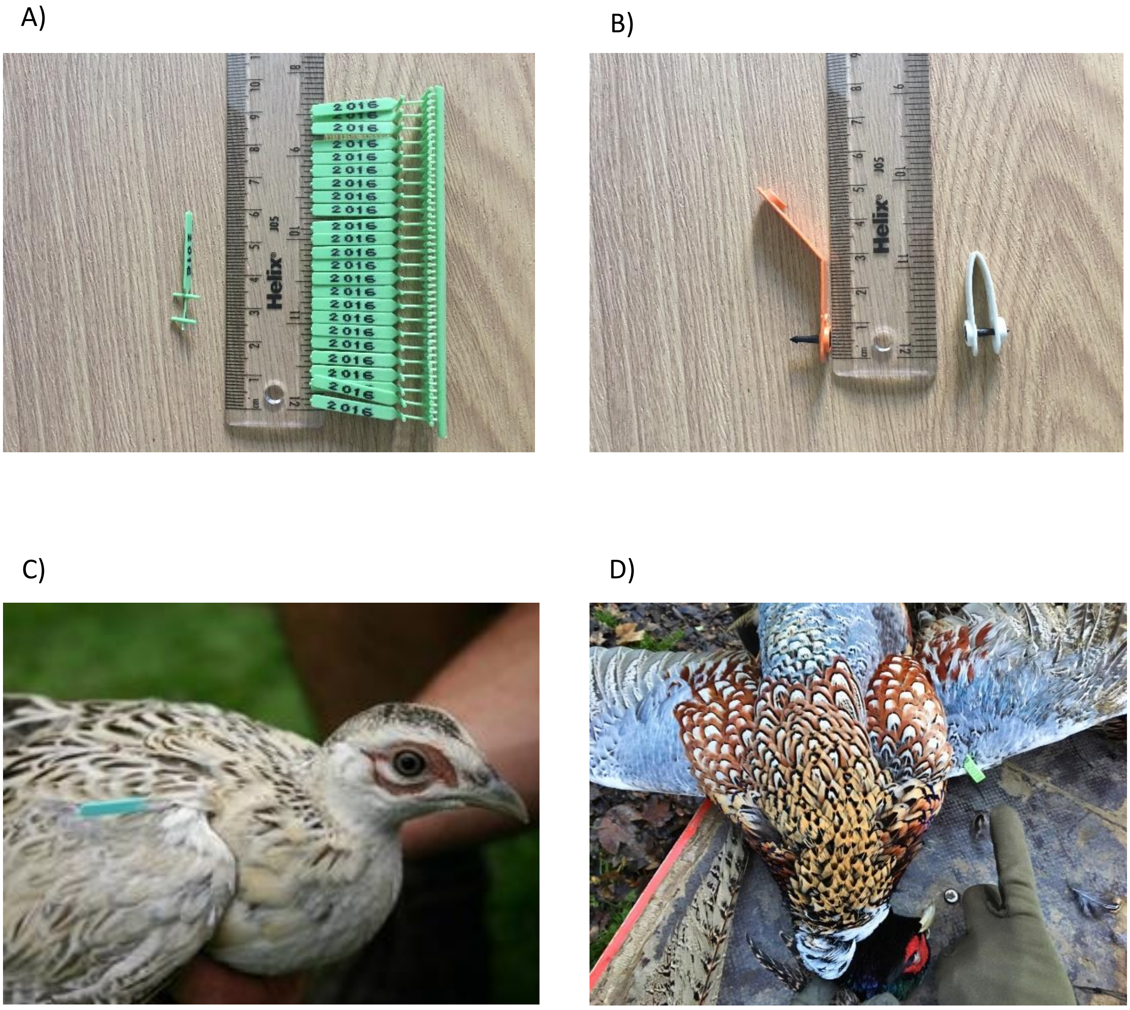

Figure 5. 1 A) Multi-Tag tag individually (left) and joined together within application bracket (right); B) Plastag unsealed (left) and sealed (right); C) Pheasant with one Multi-Tag fitted to wing (Photo provided by the GWCT); D) Pheasant with Plastag fitted to wing.

5.2.2 Tag Retrieval

We collected tags from birds during 13 scheduled driven shoots at Loddington that occurred on a weekly or biweekly basis between 80 and 175 days after release. An additional collection of tag data was carried out after the shooting season between 206-238 days after release during a separate pheasant trapping and measurements project carried out by the GWCT. During trapping, pheasants were lured into enclosed cages (2mx2mx1m) through tapering entrance tunnels by baiting the interior of the traps with grain. The tapering nature of the tunnels prevented pheasants from then exiting the cage. Cages were checked three times per day and closed at night. In total, we collected data from 832 birds that had been shot and a further 34 birds that were captured.

All birds were checked for the presence of tags by one or two individuals experienced in tag detection and counting. MTs were recorded as either being present, being damaged to the point that the dated flat had been removed leaving just the tag nub, or that they were missing entirely. The nub category was included separately because nubs can still provide useful data if they are of specific colours allocated to years or pens, but they are much more likely to be missed during a cursory search. Additionally, with the date flap lost any information (e.g. date or ID numbers) on it is also lost. Plastags we scored as either intact or missing. No instances of the equivalent of a nub were recorded for the Plastags. If both MT and Plastags were missing, we could infer that the bird had been previously marked because the Plastag leaves a noticeable circular scar of roughly 3mm which is visible after careful inspection of the pheasant wing even if the Plastag had fallen out. We carefully checked all pheasants that appeared to have neither tag to determine whether they had indeed never been tagged (and so were of no further interest to this study) or if they had actually lost both tags. No pheasants were found to have lost both tags, but in addition to multiple instances of Plastags being missing with an intact MT remaining, there was one case of a MT nub being present with a corresponding scar from a missing Plastag. Therefore, we are confident that we detected accurate deterioration rates for both tag types.

5.2.3 Statistical Analysis

Results were analysed in R version 3.6.1 (R Core Team, 2018) using binomial Generalised Linear Models with a logit link function in the package lme4 (Bates et al, 2015). Three separate models were produced. The dependant variable for the first was the presence (including nubs) or absence of MTs. The dependant variable for the second was the presence of intact MTs compared to their absence and those reduced to nubs. The dependant variable for the third model was the presence or absence of Plastags. The single independent variable in each model was Days Since Release, showing the number of days since the shot pheasant had been tagged and released, which ranged from 80 to 238. This produced models that determined whether there was a significant decrease in the probability of detecting an intact tag over time, and if so, by how much per day after release.

A single model was also produced with tag presence or absence as the dependant variable and Tag Type (Intact MT, MT Nub, and Plastag), Days Since Release, and the Tag Type:Days Since Release interaction as independent variables. However, this model structure had lower AIC when the interaction was removed, thus predicting that all tags deteriorated at the same rate over time but that they each had a different likelihood of being tagged on 0 Days Since Release. As each bird was individually tagged at 0 days since release with 100% reliability, this result was a physical impossibility. As such, the individual models were selected for the analysis as they demonstrated the real-world effect of tags deteriorating at differing rates over time.

Although our data only extended to 238 days after tagging, we used the model to predict tag durability beyond this point to the start of the following shooting season (estimated here as 450 days after initial tagging) to estimate a broad rate of deterioration between years. As this extends far beyond data collection, the predictions and standard errors become increasingly unreliable and should only be taken as a rough estimate, used to make further comparisons between tag classifications but not to determine correction factors.

5.2.4 Applying a Correction Factor to Account for Tag Loss to Reported Tag Returns from Simulated Shoots

In order to explore how tag failures may distort our understanding of harvest efficiencies, we calculated a correction factor and applied it to tag returns from simulated shoots. We generated correction factors from the decay curves obtained above. We then applied this to four simulated shoots that shot 5, 10, 15, or 20 times a season. As the results from this section will be given in the % difference between the number of tagged birds harvested and the expected number of tagged birds had tags not been lost, the number of birds shot on each shoot-day did not matter as long as it was consistent between shoot-days, e.g. 100 tagged birds shot each shoot-day. The simulated shooting season was 100 days long, ranging from 80-179 days after release, and was broken into 5 blocks of 20 days. The correction factor for a specific number of days after release was applied to the corresponding shoot-days within those blocks. For the 5 shoot-days simulation, the decay rate of Day 1 of each of the 5 blocks was applied. For the decay rate of 10 shoot-days simulation, the decay rate of Day 1 and Day 11 of each of the 5 blocks was applied. For the decay rate of 15 shoot-days simulation, the decay rate of Day 1, Day 6, and Day 11 of each of the 5 blocks was applied. For the decay rate of 20 shoot-days simulation, the decay rate of Day 1, Day 6, Day 11, and Day 16 of each of the 5 blocks was applied.

We repeated this for each of the three tag decay rates. This allowed us to compare how harvest calculations depended on different tagging techniques (MT vs Plastags) and different search strategies (cursory inspections in which only fully intact MTs would be detected vs detailed searches where any part of a MT may be detected).

5.3 Results

Of the 866 harvested or recaptured pheasants, 13 were missing their Plastags (but still had their Multi-tags), 1 was missing it Plastag (but retained an MT nub), 51 were missing the MT completely (but still had their Plastags), and 132 were missing the MT dated flap leaving just the nub (and still had their Plastags).

5.3.1 Tag decay rates

The probability that any part of a MT tag remained in a bird exhibited an accelerating decline as the shooting season progressed (Estimate = -0.0145, Std Error = 0.00425, P = 0.0006, Fig 5.2), with a probability of 97.6% (Std Error ±0.77%) that the tag remained from application to the first day of the shooting season, but only 90.2% (Std Error ±1.78%) probability that it remained on the last day of the shooting season. The probability of it remaining until the beginning of the following shooting season (450 days after initial tagging) was 15.5% (Std Error ±17%) (Fig 5.2).

The probability of the information-bearing flap of a MT tag remaining in a bird exhibited an accelerating decline as the shooting season progressed (Estimate = -0.0196, Std Error = 0.00298, P = <0.0001, Fig 5.2), with a probability of 94.9% (Std Error ±1.06%) that the tag remained fully intact from application to the first day of the shooting season, but only 72.7% (Std Error ±2.7%) probability that it remained fully intact on the last day of the shooting season. The probability of it remaining fully intact until the beginning of the following shooting season (450 days after initial tagging) was 1.32% (Std Error ±1.18).

The probability that the Plastag remained intact did not significantly decay over time (Estimate -0.0136, Std Error = 0.00793, P = 0.0861, Fig 5.2), implying that the likelihood of any part of a Plastag remaining in a bird was constant as the shooting season progressed. Despite this lack of significance, Plastag decay rates were still predicted and graphically presented to enable visual comparison. The model predicted a probability of 99.3% (Std Error ±0.403%) that the Plastag remained from application to the first day of the shooting season, and a 97.4% (Std Error ±0.912%) probability that it remained on the last day of the shooting season. The probability of the Plastag remaining until the beginning of the following shooting season (450 days after initial tagging) was 49.1% (Std Error ±60.2%).

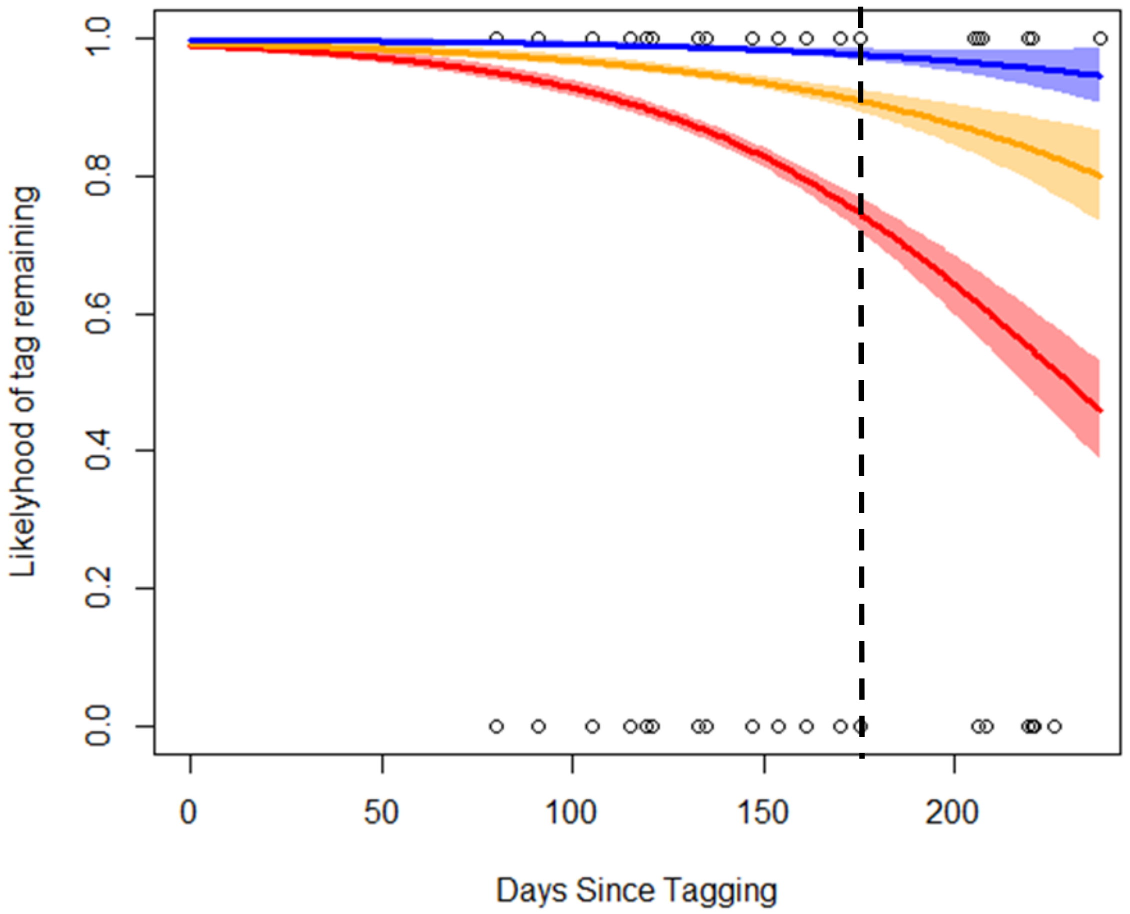

Figure 5. 2 Decreasing tag durability from day of tagging to the end of data collection (238 days after tagging) with the likelihood of a tag classification being present ranging from 1.0 = 100% likelihood to 0.0 = 0% likelihood (Plastags = Blue. MT Nub + Intact MTs = Orange. Intact MTs alone = Red). Dashed line represents the end of the shooting season. Clear circular dots represent days when data was collected.

5.3.2 Applying correction factor to hypothetical shoots

We calculated a correction factor that accounted for the increasing probability of total MT loss over the duration of the shooting season, such that for the number of tags collected on a specific number of days since application we could estimate how many other tags should have been recovered but had been lost. When we applied the correction factor to a range of simulated shoots that differed in the number of days that they shot over a season, we found that on average tag returns within the first season after tags had been applied were underestimated by 14.7% (Std Error

±1.17%) for counting only fully intact MTs, 5.2% (Std Error ±0.83%) for those that counted both Intact MTs and MT nubs, and 1.3% (Std Error±0.45%) for those that used Plastags (Table 5.1).

Shoot-days per season		Intact MTs	Intact + Nub MTs	Plastags
5	% Underestimation	13.4	4.88	1.24
	% Std Error	1.13	0.806	0.436
10	% Underestimation	14.9	5.26	1.34
	% Std Error	1.17	0.819	0.456
15	% Underestimation	14.9	5.25	1.33
	% Std Error	1.17	0.839	0.455
20	% Underestimation	15.7	5.46	1.38
	% Std Error	1.20	0.860	0.468
Average	% Underestimation	14.7	5.2	1.3
	% Std Error	1.17	0.83	0.45

Table 5. 1 % underestimation of total tag counts across shoots of differing numbers of shoot-days for Intact Multi-Tags, Intact + Nub Multi-Tags, and Plastags.

5.4. Discussion

The pattern of tag retrievals clearly shows that Plastags are more durable than Multi-Tags (MT), both when MTs are intact with the date flap remaining and when MTs are damaged with just the nub remaining. The decreasing survival of MTs over and beyond the shooting season indicated that losses persisted and indeed accelerated with time. This suggests that the tags were susceptible to ‘wear and tear’, becoming progressively weaker over time. This pattern of accelerating losses was not seen with Plastags, suggesting that their loses were primarily incurred soon after release, perhaps due to inappropriate application, and that those tags which were well-fitted persisted for several hundred days. The rates of loss that we detected and the associated noise in such measures suggests to us that after >1 year MTs provide a very poor method to record release data about a bird, with a rough estimate of only 1.32% (±1.18%) retaining an intact dated flap by the start of the following shooting season. As such, MTs should not be used in long term (>1 year) monitoring studies. Plastags remain at a much higher rate 49.1% (±60.2%), but the high standard error means that more work should be carried over time periods beyond that of this investigation to gain more accurate rates of tag decay between years. By applying these predicted rates of tag loss to model harvest returns, we estimate that current calculations of harvest rates of released birds using MTs may be up to 14.7 (±1.17%) lower than actual rates if a cursory inspection is made of harvested carcases (in which the nubs may be missed), although this may improve to 5.2% (±0.83%) if a more detailed inspection is made (such that all nubs of MTs are detected). When more robust Plastags are deployed, it leads to a much lower error of 1.3% (±0.45%). Therefore, using inappropriate tags for population monitoring can distort the understanding of a game manager about the efficiency of their release program and may encourage them to release excessive birds in future years to try to boost harvest rates. It may also lead to an overestimation of the immigration of gamebirds into a specific shoot from neighbouring shoots that do not tag their birds and/or the contribution that wild-born, untagged birds make to the harvest.

Our study shows that, depending on the tag used, patagial tagging can perform even better than the far more costly PIT Tags (Oregon RFID, 2018). PIT Tags, which are being used increasingly for marking animals (Harper and Batzli, 1993; Yates, 1997), show 5% deterioration over 12 weeks when applied to 6 week old gamebirds that were harvested in the same manner as those in our study (Carver et al. 1999). Our study shows that, over the same time period, deterioration rates are 5.4% for intact MTs, 2.6% for MT nubs, and just 0.8% for Plastags. However, although Plastags are far cheaper than PIT Tags, they themselves are more than three times more expensive than MTs, but this must be put into a broader context. MTs cost £3.25 for 100 (Perdix Wildlife Supplies, Warwickshire, UK, 2018), while the cost for the same number of Plastags is £10.32 (Roxan Ltd, Selkirk, UK, 2018). However, the cost of 100 pheasants to a shoot as of 2018 is ~£1241.00 (Game and Wildlife Conservation Trust, 2018). When taken into account, the increase in cost of tagging from 0.262% to 0.832% of the total cost of rearing, releasing, and maintaining each bird is negligible, yet providing better tags could lead to more accurate data on harvest levels and pheasant dispersal patterns. Such improvements in data accuracy could lead to more efficient pheasant management by the shoot releasing the birds, ultimately reducing the number of birds required to meet desired harvest rates and reducing overall costs. Indeed, an improvement in predictive power that enables a shoot to release just one fewer bird would fully recover the costs of tagging 100 birds via either method.

Inaccurate data is not just costly and detrimental to the individual shoot, but it could confound findings from studies with a broader scope, such as the National Game Marking Scheme (NGMS). The deterioration of tags shown in this study would not affect investigations that compared tag return rates from different pens within the same shoot (such as that carried out in Chapter 2), as all tags will likely have been affected by the same rate of deterioration if they were tagged on the same day. Where our correction factor would become useful is in absolute measures of harvest, where tag returns are compared to total harvest counts or against tag returns from shoots that released significantly earlier or later. Studies like the NGMS aim to provide figures on the number of birds released at a shoot that contribute to that shoot's harvest, with non-tagged birds assumed to be immigrants from other shoots or wild birds. By applying our correction factor, the number of wild or immigrant birds within the harvest will be reduced. This will improve both the accuracy of results and potential management that said results could inform. It would also improve the national release/harvest rates, the calculation of which is one of the primary aims of the NGMS. Using the preliminary overall yearly tag/harvest rates of the NGMS (GWCT, unpublished) and applying the average values for Intact MTs and MT nubs from Table 5.1, we can make rough estimates at the increases in the NGMS's national tag/harvest rates that the correction factor would produce (Table 5.2). Additionally, overestimating wild pheasant populations would not only provide inaccurate data on the health of wild populations, but it could also lead to less efficient management of released pheasants, potentially resulting in smaller harvest rates and larger release sizes. This would be caused by shoots diverting resources away from supporting their released birds to accommodate wild birds that simply do not exist, such as providing supplementary feed to improve pheasant breeding success (Draycott *et al.*, 2005) or increasing habitat designed to retain territorial males during the breeding season (Hoodless *et al.*, 1999).

Year	Recorded tag/harvest %	Corrected tag/harvest % if only recording Intact MTs	Corrected tag/harvest % if recording Intact MTs and nubs
2009	27.8	31.9	29.2
2010	28.1	32.2	29.6
2011	29.1	33.4	30.6
2012	31.6	36.2	33.2
2013	36.8	42.2	38.7
2014	17.8	20.4	18.7
2015	12.4	14.2	13.0

Table 5. 2 Table 5.2 Preliminary yearly result of the NGMS showing the percentage of released tagged pheasants that were then harvested, the percentages corrected for recording only fully intact MTs, and the percentages corrected for recording both intact MTs and MT nubs.

Conclusion

We conclude, based on our findings, that MTs should not be used for monitoring the contribution of previous year's birds to the harvest and only used on those birds tagged that year, and then only when a correction factor is applied. One such study that used MTs was Turner (2007) who measured both first and second year bird contribution to harvests, primarily in relation to the effect that pen stocking density has on first year harvest contribution. Turner presumed that there may be durability issues with MTs and so she placed one MT in each wing. By using our average value from Table 5.1 we calculate that this double tagging method would have been effective for first-year tags, with an average underestimation calculated at only 2.16%. This means that, by double tagging, the effect of tag decay between tagging and the first shooting season can be largely counteracted. However, Turner then calculated that <1% of previous year's birds contributed to the harvests using MTs, although it was acknowledged that this would likely be an underestimation due to tag deterioration. Even taking our model's year-to-year tag deterioration rate as a very rough estimate, as we suggest, we can indeed say with a high degree of certainty that Turner’s <1% figure may be significantly underestimated. The effect that this might have would be that a shoot believing that their harvest relied little on previous year’s birds would put little if any effort into management to retain pheasants after their first shooting season, as this would simply not be cost effective. If in reality the contribution of older birds were significantly higher, then efforts to support those birds between years might be encouraged, not only reducing the number of pheasants that would need to be released the next year directly but also potentially bolstering the wild breeding populations of gamebirds with benefits for other farmland species brought about by the associated habitat management (Donald, Green and Heath, 2001).

Although a theoretical correction factor for year-to-year tag deterioration could be developed for MTs from our models, the fact that our data collection does not extend beyond 238 days after release means that any predictions of tag durability made beyond this point will grow less accurate with every successive day. With the start of the second shooting season occurring roughly 450 days after release, our predictions of tag durability at this point are likely inaccurate and serve only as a broad estimate. Indeed, from personal experience on a 2500 release shoot that harvests ~150 pheasants per shoot day, we are aware that multiple MTs from previous years appear in the pheasant harvest at a rate of ~2 per shoot-day. A correction factor derived directly from our models would equate each of these tags as representing 76 previous year’s birds in the actual harvest, a number which is far higher than the actual numbers of untagged pheasants harvested on each of those shoot-days. As such, we can only recommend that our correction factor be applied to data that falls within the period of time of our data collection, here between 80-238 days after tagging. We also recommend that any future studies wishing to make reliable estimates of the contribution of previous year’s birds to the harvest use tags that have been proven to be more durable, such as the Plastag. However, the Plastag itself is not 100% reliable, and so we suggest that any future studies that wish to record patagial tags over longer periods of time (>1 year) should carry out a similar investigation as we have here over this longer time period. This could be done by placing Plastags or their equivalent in one wing and an even higher quality tag in the other wing to calibrate reliable correction factors. An example of an extremely durable tag would be Darvic colour rings, which have been used extensively in research and monitoring of shorebirds and have been found to be viable for up to 17 years (Ward, 2000).

Chapter 6: Can aging pheasants via the Proximal Primary Method be improved?

Abstract

Determining the age demographics of animal populations is essential when designing and monitoring different management strategies. Various methods exist for determining the age of pheasants (*Phasianus colchicus*), but the accuracy, effort required, and times of year when they can be effectively used can vary greatly. The Proximal Primary Method (PPM) involves removing one of the proximal primary feathers from a pheasant and measuring the shaft's length and diameter to differentiate between juvenile birds who have yet to moult their first adult set of primary feathers and mature birds that have. This method requires a known-age subsample to calibrate, but can be used on living or dead pheasants, can be carried out accurately any time of year outside of the breeding season, and can have data collected quickly by non-specialists. This study investigated if PPM could be improved by adding feather mass as an additional variable and by using machine learning to train a classification algorithm based on the known-age subsample.

Adding Mass significantly increased PPM's ability to age pheasants overall by 1.3%, and specifically increased accuracy of aging mature birds by 1.5% and juveniles by 1.1%. However, using machine learning produced less accurate results that other methods of PPM both when using pre-existing machine learning algorithms and a custom-built ensemble model. We recommend that feather mass be added to feather shaft diameter and length for future PPM investigations due to the ease at which it can be measured during traditional PPM feather processing.

6.1 Introduction

Determining the age structure of populations of animals is essential for effective management. Animals of different ages can have different ecological requirements, such as the need for nesting habitat for animals old enough to breed (Newton, 1994) or young animals having differing diets (Hamilton and Barclay, 1998). As such, understanding the age demographics of a population can be crucial for increasing the efficiency of management carried out to support that population. With regards to released game species, identifying the most appropriate management is often even more important as, to accommodate hunting interests, far greater numbers are being release than the land could support naturally (Díaz-Fernández *et al.*, 2013), and so maximising the efficiency of management is essential for providing the numbers of those animals that are required to sustain hunting practices. For pheasants (*Phasianus colchicus*), determining the number of older pheasants in the landscape is particularly important for selecting appropriate management to both increase the land's capacity to support older birds and to improve the likelihood of breeding success. Examples of this can be seen in predator control significantly reducing nest predation (Draycott *et al.*, 2008), breeding success increasing by providing supplementary feed in spring (Draycott *et al.*, 2005), and increased densities of male territories when supplementary feed is provided (Hoodless *et al.*, 1999). As only 16% of released pheasants survive to the end of their first shooting season (Sage *et al.*, 2018) and as little as <1% of birds released in previous years contribute to the harvest of later years (Turner, 2007), much of pheasant management is designed solely to increase survival of individuals from their release to the end of the shooting season. However, some shoots actively try to increase the numbers of pheasants surviving between years to bolster the harvests directly, by having more of the previous year's birds available to harvest, and indirectly, by increasing the number of pheasants available to breed and bolster wild bred pheasant populations. Both effects would result in fewer pheasants needing to be released to achieve the same harvest rates. By determining the age demographics of pheasant populations, shoot managers can measure, evaluate, and increase the efficiency of the management they are carrying out to maximise their ability to strengthen adult populations with the limited resources they have available. Additionally, aging the wild pheasant population can provide a useful measure of the overall health of the wild population by determining how many are surviving to adulthood.

The poor survival of pheasants that are reared and released by humans (A. P. Leif, 1994), and the fact that surviving adults generally share common requirements regardless of age, means that fine-scale differentiation of pheasant ages is of little use. Thus, it is acceptable to classify individual pheasants into one of two crude age groups; juveniles younger than one year and matures (adults) older than one year (Woodburn *et al.*, 2009). Tagging is the process of marking pheasants in some way, such as patagial tagging, so that when they are harvested or recaptured at a later date, data about the birds, such as release location or date of release, can be recorded and used to inform researchers and managers. However, as Chapter 5 discussed, the use of inappropriate tag types can lead to high rates of tag loss. This can lead to poorer data collection that can miss-inform researchers and managers regarding the status of pheasant populations, particularly for data on year-to-year survival rates which are dependent on tags remaining intact over long periods of time. Additionally, pheasants must have already been tagged prior to data collection for tagging to work. In a wild population, a population that was not tagged, or pheasants that have lost their tags, other methods of aging must be found. Several relatively accurate methods for aging pheasants have been developed, each with their own strengths and weaknesses (Table 6.1).

Method	Precision	Accuracy	Restrictions	Reference
Weight of eye lens	Pre and post 7-8 months of age.	No accuracy given. Merely that lens weights between age classes differed significant.	Must be carried out on dead pheasants. Requires specialist knowledge and equipment.	(Dahlgren, Twedt and Trautman, 1965)
Can the beak support the weight of the birds?	Pre and post 12 months of age.	86.6-94.4% for Mature. 85.1 - 100% Juvenile.	Must be carried out on dead pheasants. Less effective on heavier birds, which pen-reared birds are. Current accuracy only tested for wild pheasants 70+ years ago.	(Linduska, 1943, 1945)
Spur Length	pre and post 7-8 months of age.	80% Mature. 99% Juvenile.	Only useful on males. No use past December.	(Gates, 1966)
Burse of Fabricus depth	pre and post 7-9 months.	90%.	No Use past January. Not recommended on live birds. Requires specialist knowledge.	(Linduska, 1943)
Proximal Primary Feather	Pre-Post first breeding season.	92-98% Males. 90-92% Females.	Requires a known-age sub-sample to calibrate.	(Greenberg, Etter and Anderson, 1972; Woodburn *et al.*, 2009)
Full body metrics including: weight, tarsus length, head length, spur length, proximal primary diameter and length.	Pre-post first breeding season.	95% Males. 83-94% Females.	Requires the collection of many biometrics. Requires specialist knowledge. Requires known-age subsample to effectively calibrate.	(Woodburn *et al.*, 2009)

Table 6. 1 Techniques previously deployed for aging pheasants

Eye lens weight provides an accurate indicator of pheasant age of below or above 7-8 months (Robert B . Dahlgren, 1965) but requires the bird to be dead and specialised equipment and analysis, such as storing the eye in formalin solution for 3-12 weeks before extracting the lens, 72 hours of oven drying, and weighing to an accuracy of 0.0001g (Robert B . Dahlgren, 1965). Testing the strength of the jaw is a technique that can be used on dead birds by non-specialists, with juvenile beaks being less durable and unable to support the weight of the pheasant's body when lifted by the lower mandible (Linduska, 1945). However, this method was last tested on wild pheasants over 70 years ago, and birds from pen-reared stocks are not only heavier in general (Robertson, Wise and Blake, 1993) but it has been suggested that the current release and captive breeding systems have led to pheasants becoming larger over time (Robertson *et al.*, 2017). Heavier pen-reared pheasants would likely impact the accuracy of aging pheasants based on the amount of weight that their lower mandible can support, and as this method has not been re-tested in the past 74 years or on pen-reared stocks, the current accuracy of the jaw strength test cannot be confirmed. Measuring spur lengths is common for aging males and can be done on live birds, with errors of 20% for mature birds and 1% for juvenile (Gates, 1966), but this method is rarely used on its own due to fluctuations between populations (Stokes, 1957) and its lack of reliability into winter as the shorter juvenile spurs lengthen and begin to overlap with the longer spurs of mature birds (Woodburn *et al.*, 2009). A fairly reliable method that has been tested multiple times and used as a baseline against which other aging methods are tested is the depth of the Bursa of Fabricius (Linduska, 1943; Kirkpatrick, 1944; Siegel-causey, 1990). In juveniles, this small cavity is usually between 15-40mm deep (Woodburn *et al.*, 2009), but it is either completely sealed or very shallow in adults. However, the effectiveness of this method drops significantly by January due to juvenile depth overlapping with mature, and again, this method requires specialists to collect the data as well as analyse it. The collection of several biometric values to use as a baseline from a known-age sub-sample can accurately estimate pheasant age for an unknown age sample via multivariate discriminant function analysis (Woodburn *et al.*, 2009). Such biometrics include body weight, tarsus length, head length, spur length, ratio of body weight to tarsus length and head length, and proximal primary feather length and diameter. Using these metrics, pheasants have been aged with 95% accuracy in males and 83-94% in females (Woodburn *et al.*, 2009). This method can be carried out on dead or living pheasants, but the collection of so many specific biometrics requires significant time and specialist knowledge from the surveyor and usually requires a known-age subsample to calibrate the age classification (Woodburn *et al.*, 2009). This known-age subsample is necessary, as opposed to a single measure for all pheasant populations, as the variance in biometrics between populations can be large depending on various factors. Such factors include differing pheasant strains varying significantly in weight and morphology (Bagliacca *et al.*, 2008) and differing rearing techniques impacting various morphological features (see Chapter 2). Because of this, a known-age subsample of each individual population must be known to produce a biometric baseline to compare the larger unknown sample against (Woodburn *et al.*, 2009).

Woodburn et al (2009) found that the length of the proximal primary feather and its diameter at the shaft cuticle scar-line (Fig. 1) alone were accurate predictors when used in multivariate discriminant function analysis. This is because, as a post-juvenile feather, the proximal primary is fully grown by 10-11 weeks of age and retained until the bird’s first breeding season (Westerskov, 1957). However, despite having post-juvenile feathers, the pheasant is still not fully grown by the age of 10-11 weeks. When the feather is moulted again by the mature bird, the feather that regrows is larger than that grown by the 10-11 week old (Wishart, 1969). Other studies have also found length and diameter of the proximal primary feather shaft can provide accurate age predictions (Wishart, 1969; Greenberg, Etter and Anderson, 1972). This method can be performed on live or dead pheasants, and (as with collecting a broader range of biometrics) if a known age subsample has already been taken, extensive samples of proximal primary feathers can then be collected by someone with limited experience and sent to specialists for analysis, greatly increasing the scope of data collection and reducing time and cost. However, it does require that feathers be dried in some manner prior to measuring to remove excess moisture (Woodburn *et al.*, 2009). The need for the known-age subsample is the method’s primary weakness, but other methods, such as depth of bursa (Linduska, 1943; Siegel-causey, 1990), can be used to accurately age the subsample and collect the necessary data to form a baseline for juvenile and mature proximal primary feather lengths and diameters, allowing the proximal primary feathers alone to be collected to age any additionally sampled pheasants from that same population. The Proximal Primary Method (PPM) has the potential to provide a fast method of sampling data that can be largely carried out by non-specialists once a small sub-sample has been accurately aged, but in no previous study has the feather mass been taken as an additional variable to diameter and length. Additionally, the three primary studies that examine PPM (Wishart, 1969; Greenberg, Etter and Anderson, 1972; Woodburn *et al.*, 2009) only provide overall accuracies for the methodology and not individual accuracies for juvenile and mature birds, such as have been done for spur length (Gates, 1966). Due to this, we are unable to determine if the method is biased towards one age classification.

The current methods of PPM already have a high degree of accuracy (90-98%), but increasing the accuracy by even a little could prove extremely useful when sampling from populations with high numbers of released pheasants due to their disproportionate number of juvenile birds (Turner, 2007). In Woodburn et al's (2009) four unknown-age samples, they predicted that mature pheasants composed 32%, 13%, 17%, and 17% of their samples. However, even if Turner's (2007) prediction of <0.1% mature pheasants in the harvest were underestimated by a factor of 10 (due to tag losses), mature pheasants from this type of shoot would still only constitute 1% of the harvest. This means that even a very small percentage misclassification of juveniles could have a disproportionate effect on the numbers of predicted mature birds. That is why increasing PPM's accuracy, specifically for correctly identifying juveniles, could prove crucial for determining the overall juvenile/mature populations of an entire population and analysing any effects that changes in management might have on mature populations.

From personal experience, we are aware that feathers from mature birds often feel structurally stronger when being handled, with greater amounts of pressure needing to be applied on the lower shaft before any 'give' is felt, but no previous research has been carried out to test this. As one of the greatest strengths of PPM is that feather length and diameter can be collected swiftly and by non-specialists, we suspected that if the increase in feather shaft strength were linked with an increase in density, then it may cause a corresponding increase in feather mass, which can be swiftly and easily recorded using accurate digital scales. Why feather mass has been overlooked from previous studies, we do not know.

Supervised learning is a common form of machine learning that uses criteria of known-groups as training datasets to calibrate Machine Learning Algorithms (MLAs) that can then be deployed to classify unknown-groups (testing groups) based on those same criteria (Kotsiantis, Zaharakis and Pintelas, 2007). This method offers novel advances in data analysis over traditional methods by considering multidimensional metrics and non-linear relationships between variable to improve the accuracy at which they can be placed into groups. Machine learning can be used to classify organisms based on morphological characteristics, with examples being identifying healthy and defective zebrafish (*Danio rerio*) embryos (Jeanray *et al.*, 2015), judging the maturity of palm oil (*Elaeis guineensis*) fruit based on fruit thorn characteristics (Alfatni *et al.*, 2014), and classifying species of algae (Balfoort *et al.*, 1992). We believe that similar techniques could be used within the context of PPM to classify the age of a pheasant based on the metrics of feathers from known-age samples. Various machine learning algorithms have been developed that can offer different rates of accuracy in classification, and the method through which supervised learning is carried out allows for swift and direct comparisons between different algorithms to determine which is most effective (Acevedo *et al.*, 2009). Each MLA examines the values of the predictors of each sample within a larger training dataset, determines which predictor values most accurately classify the most samples into their correct group, and then applies those classification values to a smaller testing dataset to classify the samples within the larger testing dataset. Different MLAs use different methods of determining their classification values. Generalized Linear Models (GLMs) are a common MLA that use basic linear regression for first-order variables or non-linear trends for higher order variables to classify the training data into their correct groups. Those same regression formulae are then applied to the predictor values within the testing dataset to classify each sample within the testing dataset. Another commonly used MLA is Random Forests (Segal, 2004). This technique classifies groups by selecting a series of predictor values that most accurately separate the training dataset and then uses those values to form decision trees. The testing dataset is then passed through those decision trees, with the results classifying each sample within the dataset into a specific group. K-Nearest Neighbour (KNN) is another commonly used MLA (Guo *et al.*, 2003). This approach uses the differences between training predictor values to calculate 'distances' between predictor values that separate the different groups. The 'distances' in the values of the testing dataset are then calculated and compared to those established by the training data to determine which groups they fall into. Additionally, ensemble machine learning is a technique of constructing a set of classifying values based on the results of running multiple MLAs and then taking a weighted vote for final classifications from their predictions (Dietterich, 2000). The potential advantage of ensemble models is that the model might obtain better predictive performance by contrasting various MLAs than any of the constituent MLAs alone. Supervised machine learning has been shown to produce swift, automated results for morphological classifications on par with those that have previously required individual manual classification (Culverhouse *et al.*, 2003; Jeanray *et al.*, 2015), and could potentially improve classification accuracies over previous methods used for PPM. As stated, even small improvements to the accuracy of PPM could prove important for assessing the age demographics of an entire pheasant population when juveniles greatly outnumber matures, and so it is worth exploring novel methods of data analysis to try and achieve these higher accuracies.

In this study we will use supervised machine learning with a known-age sample to investigate Question 1) Can aging pheasants via the Proximal Primary Method (PPM) be improved by adding the mass of the feather to the traditionally used diameter and length. We will then ask Question 2) can a custom-built ensemble MLA further increase the accuracy over the commonly used, predefined MLAs of GLM, Random Trees, and KNN, and can the ensemble model or the best performing predefined MLA provide greater accuracy for aging pheasants via PPM than previously established methods. Improving the accuracy of PPM will enable researchers and game managers to gain a more accurate account of the age demographics of sampled populations, allowing for better planning and evaluation of the efficiency of management that favours supporting either juvenile or mature pheasants.

6.2 Methods

6.2.1 Data Collection

Samples were collected over two shooting seasons (2016/2017 and 2017/2018) from two shoots that released the same strain of pheasants reared at the same game rearer. Previous studies have shown that the year the feather was collected had no effect on PPM accuracy as long as they came from similar populations, as ours did (Greenberg, Etter and Anderson, 1972; Woodburn *et al.*, 2009), and our analysis using GLMs also showed that Year did not significantly affect Mature (Estimate = -0.358, P = 0.184) or Juvenile (Estimate = -0.125, P = 0.237) feather Length, Mature (Estimate = -0.015, P = 0.797) or Juvenile (Estimate = -0.00661, P = 0.793) feather diameter, or Mature (Estimate = -0.0125, P = 0.311) or Juvenile (Estimate = -0.00605, P = 0.16) feather mass. Feathers were taken from only male birds, as the primary collection site only released males. These males had previously been tagged at released when 7 weeks old, meaning that we were certain of their age. This resulted in known-age proximal primary feather samples from 44 Mature and 146 Juvenile male pheasants. Feathers were dried and lightly cleaned using paper towels before being placed between paper towels and put into dry storage for at least 12 months prior to analysis. However, a far swifter drying techniques was used by Woodburn et al (2009) by placing the feathers in an oven for 24 hours at 50◦C prior to measuring. This method is faster than our own and allows for feathers to be processed shortly after collection. Feathers then had any remaining material, usually mud, lightly brushed off. Any feathers that had excess material that could not be easily removed were discarded, as were those that had suffered damage. This left 40 Mature feathers and 116 Juvenile. We collected three measurements from each feather. First, feather length was measured to the nearest 1.0mm by straightening the feather and measuring from tip to tip along a ruler (Figure 6.1). Second, shaft diameter was taken at the cuticle tissue scar-line near the base of the barb in the same place as the vein (Figure 6.1), in line with other studies measuring feather diameter (Wishart, 1969; Woodburn et al, 2009). Shaft diameter was measured to the nearest 0.01mm using a measured tapering aperture that varied in length from 2.0mm to 4.5mm, upon which the feather was slid along at the cuticle scar-line as described in Robertson (1985). Finally, feather mass was measured to the nearest 0.01g using Triton T3 electron scales. With a known-age sample as a baseline, a range of machine learning algorithms were tested to train data models to predict pheasant binomially as either Juvenile (0) or Mature (1). All analysis was carried out in R version 3.6.1 (R Core Team, 2018) using the 'caret' (Kuhn, 2008) and SUPERLEARNER (Van Der Laan, Polley and Hubbard, 2007) packages.

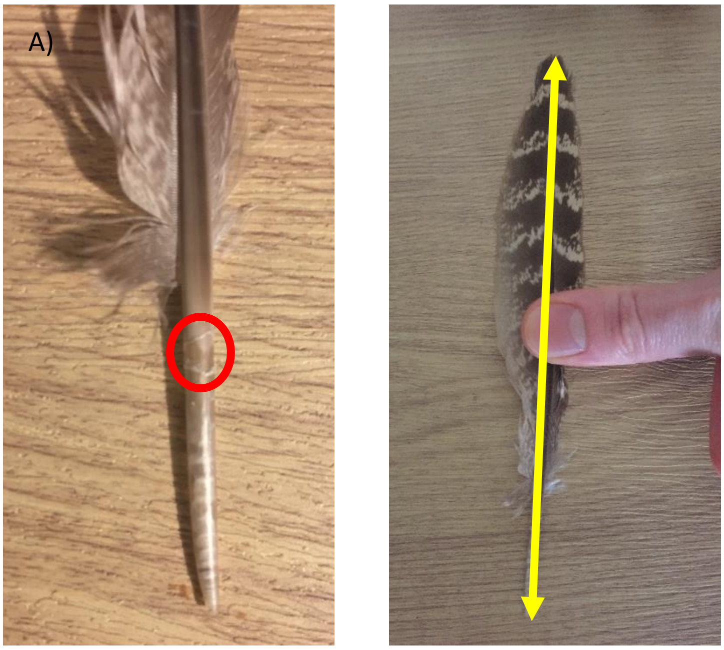

Figure 6. 1 A) cuticle scar-line (Red) where feather diameter was measured. B) length of feather that was measured from tip to tip (Yellow)

6.2.2 Statistical analysis

Prior to testing any machine learning algorithms, the data for feather Diameter, Length, and Mass was normalised so that they would be directly comparable to one another for the analysis. This was done via percentage normalisation, with the highest value in each category scored as 1.0 and all other measurements scored below that level relative to their own value, e.g. a feather with a Length measuring 90% that of the longest feather would score 0.90.

The 'caret' package was used to test three different MLAs. Caret is a package that allows for the streamlining of predictive models and enables a range of predefined MLAs to be test in a directly comparable manner by simply entering which of the predefined MLAs the user wishes to test (Kuhn *et al.*, 2013). The three model algorithms that were tested were Random Trees, KNN, and Generalized Linear Models (GLM). These were run twice, first with Diameter and Length as predictive variables and a second time with Diameter, Length, and Mass. This was done because the MLA that best predicts pheasant age using two variables may not be the same MLA that best predicts pheasant age using all three variables. Once the best MLA was established for two and three variables, they could then be compared. The data used to train each model was a random selection that accounted for ~75% of the Mature and Juvenile samples resulting in 31 Mature feathers and 87 Juvenile, while data that the models were then tested against consisted the remaining ~25% of each age class, resulting in 9 Mature and 29 Juvenile. Other studies have used a 66.6% training dataset with a 33.3% testing (Jeanray *et al.*, 2015), but such studies have had a greater total number of samples from which to train their data. Due to our smaller sample size, we increased the size of the training sample to ~75% so that a greater range of mass, length, and diameter values would be included during MLA training, hopefully increasing model accuracy.

The 2 and 3 variable models for GLM, Random Trees, and KNN are classified as V2.GLM, V3.GLM, V2.RT, V3.RT, V2.KNN, V3.KNN respectively (Table 6.1). These models were then run 310 times each using randomly selected training and testing datasets to test each over a range of samples, resulting in 11780 predictions (38x310). In comparison, another study using supervised learning to classify animals based on morphological characteristics ran their models between 5-75 times to gather more stable estimations (Jeanray *et al.*, 2015). We ran our models a far higher number of times as we believed the differences in accuracy and Kappa caused by adding feather mass may be small, similar to that added by length (Woodburn *et al.*, 2009), and so an increased sample size would provide greater statistical power to determine if the effect of adding Mass was significant. The Kappa statistic was used as a finer scale measure of overall model accuracy instead of simple accuracy. Kappa controls for the accuracy of a random classifier as measured by the expected accuracy and takes into account issues of class imbalances and is well suited to binomial data skewed towards one outcome (Ben-David, 2008). As there is a clear imbalance between the number of Juveniles and Mature feathers and our data is binomial, Kappa was considered a more reliable measure of accuracy. Kappa is scored between 0-1, and although there is no standardized way of interpreting the values of Kappa (The Data Scientits, 2016), Landis and Koch (1977) suggest Kappa values indicate the level of agreement between predictions and true values as follows: 0.0-0.2 = slight agreement , 0.21-0.40 = fair agreement, 0.41-0.60 = moderate agreement, 0.61-0.80 = substantial agreement, and 0.81-1.00 = almost perfect agreement. For our purposes will be directly comparing the Kappa results between one another.

The Kappa outputs of each of the 310 model runs for each MLA were then placed into GLMs to investigate if Kappa was significantly affected by the MLA used. In this way we could determine which of the two-variable models scored the highest Kappa, which of the three-variable models scored the highest Kappa, and then compare the Kappa scores of these two best models to determine if adding feather mass caused a significant increase to model Kappa. Additionally, we placed each MLA's total 11780 estimates and their corresponding true values into a single confusion matrix. This provided us with the total number of correctly identified Juvenile feathers, correctly identified Mature feathers, incorrectly identified Juvenile feathers, and incorrectly identified Mature feathers for each MLA. From these we could establish individual percentage accuracies for each classification to determine if our models were bias towards correctly identifying one age class over the other.

To answer Question 2, the 'SuperLearner' package was used. SuperLearner is a cross-validation package that estimates multiple machine learning model performances and creates an optimal weighted average of those models known as an ensemble (Kennedy, 2017). SuperLearner ran multiple pre-defined MLAs on the training data, assigned weighted values to each of the MLA predictions based on their accuracy, and then predicted the classifications of the testing data using those same weights.

Length, Diameter, and Mass were used as the predictors. A total of 41 different MLAs from the SuperLearer archive of predefined MLAs were tested. Those that increased model Kappa were retained while those that reduced it were removed until the structure that produced the highest Kappa was left. Those MLAs were: SL.lm, SL.randomForest, SL.ranger, SL.rpartPrune, and SL.step. The only MLAs that were consistently given any weight for predictions were SL.lm, an MLA that used linear regression on the predictors to classify the samples into groups, and SL.step, a MLA that carries out both forward and backwards stepwise regression on the predictors to classify the samples into groups. The remaining three MLAs were all variations on the Random Forests MLA that defines groups based on decision trees as described above. However, despite the Random Forest variation MLAs not appearing to influence the classification of the feather due to no weight being assigned to them in the ensemble model, removing SL.randomForest, SL.ranger, and SL.rpartPrune from the ensemble model reduced model Kappa. As such, they were retained. Every run of a new randomised training dataset assigned different weight to the predictions of SL.lm and SL.step that defined the extent to which that MLAs predictions would influence the ensemble model’s final prediction, but the range typically fell within 0.15 -0.35 for SL.lm and 0.65-0.85 for SL.step, with 1.00 being the model output results used for 100% of the predictions and 0.00 being the model outputs being used for 0% of the predictions. Models using this structure shall be referred to as the Ensemble Models.

The cut-off thresholds within the Ensemble Models is a value between 0.0-1.0 that defines the point that the model separates two classifications, in this instance whether a feather is classified as belonging to a Juvenile or Mature pheasant. This threshold can be manually altered very easily, allowing for the models to favour the identification of one classification over the other. As such, we were able to test the effects of shifting the cut-off threshold on our final Ensemble Model. The cut-off thresholds we tested ranged between from 0.10-0.90 and increased in increments of 0.10, producing 9 versions of the Ensemble Model that were structurally identical in which MLAs were included within them but with different cut-off thresholds. By shifting the cut-off threshold, the likelihoods of any one feather within one classification truly belonging to that classification could be increased, though the samples sizes would decrease. By combining low and high threshold results, a dataset can be created with three classifications: High Certainty Juvenile (all those classified as Juvenile at a threshold of 0.10), High Certainty Mature (all those classified as a Mature at a threshold of 0.90), and Uncertain (all feathers that did not fall into the High Certainty Mature or High Certainty Juvenile categories).

6.3 Results

<u>6.3.1 Which models have the highest Kappa for the two-variable and three variable models after 310 model runs?</u>

For the two-variable models, V2.GLM was used as the intercept in the GLM used to compare MLAs (Estimate = 0.530, Std Error = 0.00887, P = <0.0001). V2.RT's Kappa is significantly lower than V2.GLM (Estimate = -0.085, Std Error = 0.0126, P = <0.0001). V2.KNN's Kappa was not significantly different to V2.GLM (Estimate = 0.00733, Std Error = 0.0126, P = 0.56) (Table 6.2).

For the three-variable models, V3.GLM was used as the intercept in the GLM used to compare MLAs (Estimate = 0.573, Std Error = 0.00832, P = <0.0001). V3.RT's Kappa is significantly lower than V3.GLM (Estimate = -0.114, Std Error = 0.0117, P = <0.0001). V3.KNN's Kappa was significantly lower than V3.GLM (Estimate = -0.0237, Std Error = 0.0117, P = 0.0444) (Table 6.2).

When the Kappa values of the two equally best performing two-variable models (V2.GLM and V2.KNN) were tested against that of the best performing three-variable model (V3.GLM), V3.GLM had significantly higher Kappa than both 2V.GKM (Estimate = 0.0437, Std Error = 0.0121, P = <0.0003) and V2.KNN (Estimate = 0.0363, Std Error = 0.012, P = 0.00329). Using V2.KNN as a benchmark, as it had the highest Kappa of the two-variable models, adding feather mass increased Mean Total accuracy by 1.3%, Mature classification accuracy by 1.5%, and Juvenile classification accuracy by 1.1% (Table 6.2).

6.3.2 Can an ensemble model be produced that is more accurate than the pre-defined MLAs used in Question 1?

Kappa for the highest three-variable MLA (V3.GLM) was significantly higher than that of the Ensemble Models with the highest Kappa (Ensemble 0.50) (Estimate = 0.0247, Std Error = 0.0122, P = 0.044), showing that overall Kappa was not improved by the creation of an Ensemble Model (Table 6.2). Altering the cut-off threshold of the Ensemble Models shifts the likelihood of correctly identifying one classification at the expense of correctly identifying the other, with a maximum Juvenile accuracy of 98.6% in Ensemble 0.10 and a maximum Mature accuracy of 85.7% in Ensemble 0.90 (Table 6.3). However, these decreases in respective accuracies were caused by the narrowing of the boundaries that classify an age group, resulting in those feathers that are classified from low accuracy groups having higher overall likelihood of truly belonging to that group due to the increased requirements to be classified as that group (Table 6.3). This is demonstrated by the likelihood of a Juvenile classified feather truly being Juvenile from Ensemble Model 0.10 being 98.6% and a Mature classified feather truly being Mature from Ensemble Model 0.90 being 85.7% (Table 6.3).

6.3.3 Using the Ensemble Model, how many feathers can be classified as High Certainty Mature, High Certainty Juvenile, and Uncertain, and what are the accuracies of these higher certainty classifications?

Using Ensemble 0.10 and Ensemble 0.90, we created a dataset of; 574 High Certainty Matures, with the likelihood of each of those feathers truly being Mature at 85.7%; 4,414 High Certainty Juveniles, with the likelihood of each of those feathers truly being Juvenile at 98.6%; and 6792 feathers classified as Uncertain.

Model	**Mean Kappa**	**Kappa Std Error**	**Mean Total % Accuracy**	**Mean Total % Accuracy Std Error**	**Juvenile % accuracy**	**Mature % accuracy**
V2.GLM	0.530	0.00888	84.6	0.273	93.8	55.1
V2.KNN	0.537	0.0126	85.1	0.386	94.7	54.4
V2.RT	0.445	0.0126	80.9	0.386	89.3	53.7
V3.GLM	0.574	0.00832	86.4	0.261	95.8	55.9
V3.KNN	0.550	0.0118	85.4	0.369	94.6	55.9
V3.RT	0.460	0.0118	81.1	0.369	94.6	55.9
Ensemble 0.50	0.549	0.0087	85.5	0.265	94.7	54.4

Table 6. 2 Mean Kappa, mean overall accuracy, and absolute accuracy for individual age class results for the 3 two-variable MLAs, the 3 three-variable MLAs, and the bester performing three-variable Ensemble Model after 310 model runs.

Model	Mean Kappa	Kappa Std Error	Juvenile % Accuracy	Mature % Accuracy	% likelihood of a randomly selected feather from within the total group of Juvenile predicted feathers truly being Juvenile	% likelihood of a randomly selected feather from within the total group of Mature predicted feathers truly being Mature
V3.GLM	0.574	0.00832	94.6	55.9	87.4	76.2
Ensemble 0.10	0.300	0.00789	48.4	97.8	98.6	37.0
Ensemble 0.20	0.416	0.0112	68.9	84.3	93.4	45.7
Ensemble 0.30	0.482	0.0112	83.0	69.5	89.7	55.9
Ensemble 0.40	0.521	0.0112	90.5	60.3	88.0	66.3
Ensemble 0.50	0.549	0.0112	95.2	54.4	87.1	77.7
Ensemble 0.60	0.523	0.0112	96.7	48.9	85.9	82.2
Ensemble 0.70	0.469	0.0112	97.6	42.0	84.4	84.4
Ensemble 0.80	0.367	0.0112	98.1	30.4	82.0	83.2
Ensemble 0.90	0.274	0.0112	99.1	17.6	79.5	85.7

Table 6. 3 Mean Kappa, absolute % accuracy for individual age classes, and % likelihood of a any individual feather from within each individual age class belonging in the correct age class for the best performing MLA and 9 Ensemble Models of differing cut-off thresholds.

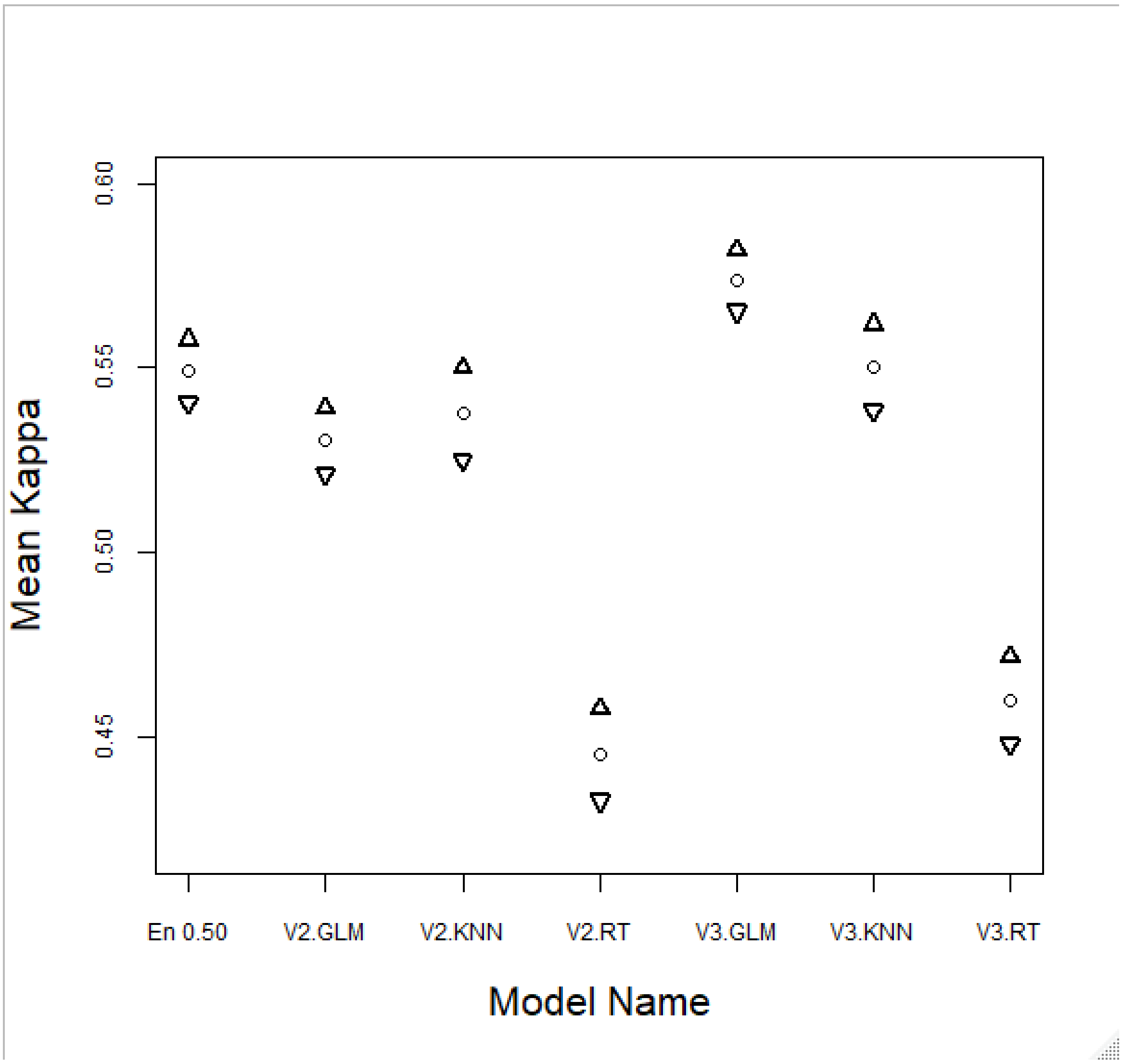

Figure 6. 2 Mean Kappa results (circles) and upper and lower standard errors (triangles) for the 3 two-variable MLAs, the 3 three-variable MLAs, and the bester performing three-variable Ensemble Model after 310 model runs.

6.4 Discussion

KNN and GLM were both equally as accurate at predicting pheasant age based on just feather Diameter and Length, with KNN having marginally higher Kappa. When feather Mass was added, the GLM MLA produced the most accurate predictions and increased overall accuracy by 1.3%, and specifically increased Mature accuracy by 1.5% and Juvenile accuracy by 1.1%. Creating a new Ensemble Model did not increase the overall accuracy above that of the predefined GLM MLA. However, by shifting the cut-off threshold of the Ensemble Model, we were able to demonstrate that it is possible to raise the criteria by which one of the ages are classified at the expense of the other, and in doing so increase the likelihood of those feathers that are placed in that classification truly belonging to that classification. This resulted in the likelihood of Juvenile classified feather truly being Juvenile in Ensemble Model 0.10 being 98.6% and the likelihood of a Mature classified feather truly being Mature from Ensemble Model 0.90 being 85.7%.

Previous studies have shown higher rates of overall accuracy when using methods other than machine learning for PPM, with Greenberg, Etter, and Anderson (1972) deriving overall aging accuracies of 92-98% for males and 90-92% for females and Woodburn et al (2009) deriving 95-98% for males and 83-91% for females, though we did not test female feathers in our investigation. However, in neither of these studies do they provide classification accuracies for Juvenile and Mature classes individually, merely an overall accuracy of the entire sample. In our study, we were able to derive separate likelihoods for each age classification, with our best two-variable PPM model correctly classifying Juveniles (95.8%) to a greater degree than correctly classifying Matures (55.9%). Because of this, we can only say that the spur length techniques (that did provide individual Juvenile and Mature accuracies) (Gates, 1966) was superior to ours at correctly classifying each age group. However, our model’s bias towards correctly identifying Juveniles could be beneficial, for reasons we will discuss below.

What this study has shown is that adding the mass of the feather significantly increases the accuracy of the predictions using MLA by 1.3% overall, and specifically by 1.5% for correctly identifying Mature pheasants and 1.1% for correctly identifying Juvenile. As such, adding feather mass will likely increase the accuracy of PPM predictions using other methods, such as discrimination analysis (Woodburn *et al.*, 2009). This increase may appear relatively small, but Woodburn et al (2009) showed that adding feather length as a second variable in their discriminant analysis only increased accuracy by between 1-3% over using diameter alone. Although the increase we demonstrated was small, it was statistically significant.

We must then ask if the effort and time required to collect the feather mass can be justified, given the small increase it produced. As feather drying can be achieved much swifter using an oven than our dry storage method (Woodburn *et al.*, 2009), the only additional time required for the collection of feather mass demonstrated by our methodology is to remove any excess mud and then weight the feather, a process that takes only a matter of seconds. As such, we deem this easily collected additional variable as worthy of adding to the standard methodology for PPM. Regarding PPM in general, the method allows for accurate separation of Juvenile and Mature birds up until the bird’s first breeding season, meaning that data can continue to be collected to the end of the shooting season and on into spring, unlike bursal depth or spur length (Linduska, 1943; Gates, 1966). In our experience, 5-10 proximal primary feathers can be collected every minute. This allows for rapid data collection, as many feathers can be collected easily from both live and dead birds. This is beneficial when taking very large samples, such as from high-release pheasant harvests. Although processing the individual feathers for length, diameter, and mass takes time, this can be done at any point after collection and drying and does not rely on storing many dead pheasants or time spent and stress induced upon pheasants by prolonged handling of live birds (Chloupek *et al.*, 2009). In this way, PPM is superior to other aging methods.

Due to the disparity between Juvenile and Mature birds that is often seen in harvests (Turner, 2007), even relatively small increases to aging accuracy could have significant effects on estimating the true number of Mature birds in the harvest. This disparity would also make it preferable to choose a model that overestimates the Juvenile population as opposed to overestimating the Mature population, as a 1% increase in Matures classified as Juveniles would affect the true total of Juvenile and Mature numbers less than a 1% increase in Juveniles classified as Matures. An example would be assessing the effectiveness of different predator control methods, as rates of predation are very high for pheasants (Sage *et al.*, 2018). Higher rates of incorrectly classified Juveniles could increase apparent Mature numbers far above their true levels, and so any positive effects that a particular predator control technique might be having on bolstering the true Mature population many not be detected, resulting in that management technique appearing ineffective regardless of whether it was or was not in reality. By increasing the accuracy of PPM by adding feather Mass, the true effect of the management would be easier to identify.

The creation of the High Certainty Juvenile and Mature dataset was done as an aside to the main investigation of this project. However, the use of such a technique would have benefits. An example of this would be when investigating individual pheasants from large datasets, such as establishing differences in weight between Juvenile and Mature birds harvested from a large pheasant shoot. In this case researchers could have a much higher degree of certainty of the true age of the pheasants they were studying and have access to a large sample size, offsetting the reduction in high certainty classifications.

6.5 Conclusion

It is our recommendation that any future work using PPM to age pheasants add the mass of the feather along with length and diameter. This will increase the accuracy of PPM by itself and likely increase the overall accuracy if PPM is just one of a range of biometric variables that are being used to age pheasants. Although the increase in accuracy was relatively small, even small increases can be very beneficial for judging the effectiveness of management techniques when the numbers of Mature birds in the sample are much smaller than those of Juveniles. The MLAs tested in this study do not achieve the overall accuracies of previous methods that have been tested, both using pre-established MLAs and ensemble models. However, MLAs could also be applied if a wider ranges of biometrics are collected in the same way that discriminant analysis is carried out, which may produce results with greater accuracy.

7. General Discussion

7.1 Thesis overview

I found that the Enhanced Rearing conditions improved harvest rates relative to Control pheasants by 16-17% on shoots releasing <601 pheasants or >2000 (Chapter 2). When release date was considered instead of release size, earlier releases harvested more Enhanced pheasants. Our model predicted the mean per-pen harvest sizes of Enhanced birds surpassing Control on release that occurred 40 days (August 22nd) prior to the legal start of the shooting season, with Enhanced pheasants harvests relative to Control increasing by 1.44% with each addition day prior to August 22nd that the release occurred (Chapter 2). Birds reared under Enhanced conditions gained weight at a rate of 0.82g per day slower than those reared under Control conditions after release, and they had relatively larger breast muscles (+7.3%), hearts (+4.46%) and tarsi (+6.2%) compared to Control birds (Chapter 2), with the increases to breast muscle and tarsi only occurring when Enhanced harvest rates were higher. Such differences in morphology, specifically weight and heart mass, may explain why Enhanced pheasants had increased flight performance when compared to Control birds when being hunted (Chapter 3). Despite being exposed to live prey early in life, resulting in Enhanced pheasants becoming better predators of such prey and having a more varied diet post-release (Whiteside et al. 2015), we found no evidence that Enhanced pheasants caused greater declines in invertebrate populations in release pens immediately following release when compared with Control birds (Chapter 4). However, pheasant releases in general did lead to some, inconsistent, declines in specific invertebrate measures in some years (Chapter 4). Like previous studies on the ecology and behaviour of released pheasants, much of our work relied on recovery of ID tags. We found that a commonly deployed tag type was very prone to damage and loss, introducing errors in estimates of recovery rates which increased with time so that by the end of the shooting season 27.3% of tags were missing their dated flap and 9.2% of tags were missing completely (Chapter 5). This also meant that after one year, these tags provided data on survival that was likely to be very inaccurate (Chapter 5). Such tag data could be improved by incorporating a correction factor to account for tag loss, or better still using a different tag type that we tested that had a failure rate of only 2.6% by the end of the shooting season (Chapter 5). We tested one way to improve a method of aging untagged birds (or those whose tags have been lost) (Woodburn et al. 1990) by considering the mass of their proximal primary feathers as well as length and diameter measures and using machine learning methods to enhance classification accuracy (Chapter 6). We could improve aging accuracy of juveniles by 1.5% and Mature birds by 1.1%.

Therefore, my thesis has acted as a case study to demonstrate how altered management procedures relating to the rearing and release of pheasants can and should be evaluated before being recommended for wider use. This reduces the chances of unintended negative ecological and ethical consequences arising following the introduction of novel methods and could help convince breeders that such methods are likely to bring tangible benefits in an economically viable manner.

This discussion summarises and examines the implications of our findings under three broad headings. 1) Wider implications of our findings; 2) Limitations of our findings; 3) Future directions for work.

7.2 Wider implications of our findings

In Chapter 2, we estimated the effects of Enhanced Rearing if it were applied to the release of 20 million pheasants. Although 39-57 million pheasants are released annually (Aebischer, 2019), my results are likely to be only relevant to a number lower than this as the benefits did not occur on shoots releasing 601-2000 birds. There is no substantive data on the number of pheasant shoots in the UK or how many each shoot releases, and as such, 20 million was chosen as a conservative figure as it would account for ~35-50% of pheasants released annually, despite the effects occurring on larger shoots which would account for the majority of released pheasants. Another reason for this conservative figure is that it is likely that these novel rearing techniques may take time to percolate into the practices of game-rearers. Research relating to game management can find difficulty in filtering into wider circulation. A primary example of this is that Greenall's (2007) found that some (though how many was not specified) of the gamekeeper in their study into the social attitudes of gamebird shooting were unaware of the existence of 'The Code of Good Game Rearing Practice' despite it being produced by the British Association for Shooting and Conservation, the Game and Wildlife Conservation Trust, and the Game Farmers' Association. Another example of a lack of implementation of knowledge is that it is widely understood that pen stocking densities, particularly those over 0.1 birds per m^2, can be detrimental to the environment in and around release pens (Sage, Ludolf and Robertson, 2005; Sage *et al.*, 2009; Neumann *et al.*, 2015; Capstick, Sage and Hoodless, 2019), but despite such research being fairly widely available by those involved in shooting (Greenall, 2007), stocking densities have not decreased. This can be seen in mean stocking densities across 53 pens in Sage, Ludolf, and Robertson's (2005) paper being 0.180 birds per m^2 while mean stocking densities in the 49 pens in Chapter 4 (12 years later) being 0.257 per m^2. It is this lack of the implementation of novel information that led to us using a conservative figure for our estimations of the overall impact of Enhanced Rearing

For some shoots, managing pheasants and the habitats into which they live and/or are released into in a way that benefits the environment is a high priority (Stoate and Szczur, 2001; Draycott, Pock and Carroll, 2002; Sage, 2007), but for those of a commercial nature, making a profit is often the overarching goal. Considering that 42% of commercial shoots made a loss in 2017/2018 (Game and Wildlife Conservation Trust, 2018), making positive environmental changes are less likely to be adopted if they add additional economic costs. In this respect at least, Enhanced Rearing is economically viable as the additional costs of rearing are significantly outweighed by the gains to harvest rates, and so Enhanced Rearing holds the potential to become widely adopted if the information can filter to game managers and rearers. However, this leads to a potentially conflicting application of our research. Simply put, if a shoot is commercial in nature, they may choose to release fewer birds and maintain the level of shooting, which is our intention, or they could exploit this methodology and so maintain releases at current levels while using

Enhanced birds and benefit from an increase in the amount of shooting. This could result in an increase in survival of Enhanced birds without a corresponding decrease in release size, resulting in an even higher density of pheasants in the landscape post-release, causing greater detrimental effects than those already seen from high density releases (Sage, Ludolf and Robertson, 2005; Sage *et al.*, 2009; Neumann *et al.*, 2015; Capstick, Sage and Hoodless, 2019). However, it is worth noting that if the levels of shooting were to likewise increase to take advantage of the higher number of available pheasants, the higher densities would begin to decline through the shooting season. Greenall (2007) found that self-regulation by shoots to prevent bad practices were highlighted as an important objective by those working on shoots, the owners of shoots, and those carrying out shooting, but they also found that those within the shooting community believed that those shoots that concentrate on short-term profits would continue to shoot excessively large numbers of pheasants or refuse to alter their practices to more acceptable formats. Considering the high number of commercial shoots that did not make a profit in 2018 (Game and Wildlife Conservation Trust, 2018), it is likely that maximising short-term profits ranks high in the objectives of commercial shoots, the very types of shoots that have driven the huge increase in pheasant release numbers over the past decades (Robertson *et al.*, 2017). In short, we cannot determine the manner in which our results will be implemented. We can merely provide the tools for releasing fewer pheasants and hope that they are put to the use for which they were intended.

Taking the mean pen stocking densities found in Chapter 4, a reduction of 16% in release numbers would reduce stocking densities from 0.257 per m^2 to 0.216 per m^2. This is still around double the 0.1 pheasant per m^2 of release pen believed to alleviate many negative effects and recommended in the Code of Good Shooting Practice (Sage, Ludolf and Robertson, 2005; Neumann *et al.*, 2015; Capstick, Sage and Hoodless, 2019). However, the negative effects on soil chemistry and ground flora both during a pen's use and after pens have been abandoned continue to increase with higher stocking densities (Sage, Ludolf and Robertson, 2005; Capstick, Sage and Hoodless, 2019), as do some of the negative effects on invertebrates (Neumann *et al.*, 2015). As such, although Enhanced Rearing would not reduce stocking densities to the point where no or little damage is done, it would likely still reduce the amount of damage to the pen environments caused by pheasant releases. We can demonstrate this using our own models for interior total invertebrate biomass (Chapter 4), with our model estimating that the density reduction of 0.257 birds per m^2 to 0.216 birds per m^2 would increase total invertebrate biomass by 3.36% inside the pen prior to release. In this way we can show how the reduction of release densities caused by Enhanced Rearing could directly reduce one of the negatives effects of pheasant releases. Increasing the invertebrate biomass within release pens could be beneficial for conservation if invertebrates of conservation concern are located close to release pens (Callegari, Bonham and Holloway, 2014), if animals that rely on them as prey are of conservation concern, such as hedgehogs which are in a steep national decline (Hof, 2009), or if bolstering the invertebrate populations aids in the rate of turnover of organic matter and nutrient cycling (Edwards, Reichle, and Crossley, 1973).

We also found that increased pheasant stocking densities increase slug abundance both inside and outside of release pens. Implementing a 16% decrease from our mean pen stocking density again could lead to an 8.37% decrease in slug abundance in and immediately around release pens. This could benefit neighbouring arable farming, as 12 and 24 slugs per m^2 of wheat during autumn can cause 12% and 20% losses in seedlings number respectively and 46% and 70% losses respectively during winter (Barratt, Byers and Bierlein, 1994). As such, Enhanced Rearing could not only be cost-effective for shoots but also benefit farms where release pens are in close proximity to arable crops, both increasing crop yields and reducing the need for pesticides.

The release of Enhanced birds could have two potential effects on predator populations. First, the release of gamebirds may increase inter-annual generalist avian predator population growth (Pringle *et al.*, 2019), and it is possible that the same occurs with fox population. A reduction in release numbers could lead to declines in such predators in the long term, due to decreased food abundance. The direct effects of declines in populations of common generalist predator species, such as jays and magpies, would be of little conservation concern, but for species of specific conservation concern that feed on pheasants, such as red kite (*Milvus milvus*) (Pain *et al.*, 2007), the loss of an abundant and easily attainable food source could be detrimental. However it is worth noting that species such as red kites often feed on wounded or un-collected birds that have already been shot (Pain *et al.*, 2007), and as releasing Enhanced pheasants would not decrease the actual number of birds being shot (and subsequently the numbers being wounded or un-collected) then it should only decrease the availability of pheasants as a prey item to animals that are actively hunting fit, living birds. A reduction of generalist predator numbers may also have positive effects for other prey species, such as reducing the negative effects that crows can have on the productivity of other bird species (Madden, Arroyo and Amar, 2015; Sage and Aebischer, 2017) and the effects that fox predation can have on small mammals (Reynolds and Tapper, 1995). In this way, Enhanced Rearing could have additional indirect benefits for wildlife.

The second effect that the release of Enhanced birds might have on predators is a reduction in predator control. Predator control as a management strategy is usually carried out when predators are having a significant negative effect on the gamebird population (Tapper, Potts and Brockless, 1996). The primary manner in which Enhanced Rearing is likely to have improved pheasant survival is by increasing the propensity of birds to roost off the ground, reducing their mortality due to predation (Whiteside, Sage and Madden, 2016; Santilli and Bagliacca, 2017). By reducing losses due to predation, shoot managers may be less motivated to carry out predator control. This could potentially be detrimental to other species which benefit from such predator control (Sage and Aebischer, 2017). However, as predator control can prove a divisive issue with regards to the ethics of shooting and land management in general (Talbot, 2003), this could help reduce tension between those for and against pheasant releases; though the differing opinions on the actual shooting of pheasants would still be present. Additionally, reducing predator control would save shoots funds and resources that could be redirected towards other aspects of management.

Regarding ethics, moral arguments prove an important component in legitimizing hunting practices in the opinions of conservation practitioners, game managers, and the public (Fischer *et al.*, 2013), and although hunting practices that are considered ‘moderate’ and ‘measured’ foster far less contention between pro and anti-shooting groups, there is a lack of perceived legitimacy for ‘excessive’ hunting practices (Fischer *et al.*, 2013). The release of 39-57 million pheasants each year (Aebischer, 2019) on shoots where hundreds of birds may be shot per shoot-day may, for some, place pheasant shooting squarely into the excessive category. Additionally, any argument justifying the current levels of commercial pheasant shooting as a method of providing game meat are questionable, as the current market for game meat is so saturated that the price shoots make per bird sold to game dealers decreased by 50-60% between 2011-2017 (Game and Wildlife Conservation Trust, 2018). The rearing, release, management, and shooting of pheasants is done as a sport above all else, and the practice of releasing gamebirds has been shown to be disliked by the majority of the public when it was studied in Denmark (Gamborg, Jensen and Sandøe, 2016). From a UK perspective, Greenall (2007) found that gamekeepers were the only stakeholders involved in shooting that did not have concerns about large-scale releases and excessive harvests, and those who ran small shoots had a tendency to dislike larger commercial shoots that could sometimes undertake unacceptable practices. To quote directly, ‘Some shoot owners were annoyed that those who adopt negative practices benefited financially and would not change their ways even if it meant the demise of gamebird shooting’ (Greenall, 2007). One method that would reduce the negative impacts, both environmentally and ethically, of large-scale pheasant releases is banning releasing pheasants altogether and only shooting wild pheasants. Surprisingly, Greenall (2007) showed that the only group involved in shooting that would readily accept a total ban on the rearing and releasing of gamebirds was gamekeepers, as they would find it preferable to re-focus their profession to supporting wild populations for shooting. This, coupled with the responses from other stakeholder that Greenall (2007) found, shows that at almost all levels within the shooting community itself there is a desire to improve shooting practices, and Enhanced Rearing offers a method through which release sizes can be reduced if it is used responsibly.

There is also a broader environmental aspect to consider regarding the potential impacts of our Enhanced Rearing methodology. Direct figures on the CO2 footprint of rearing and releasing pheasants under current commercial conditions could not be found, but would involve the heating of sheds, feed production, transportation to rearers and then shoots, building and maintaining release pens, constant filling of feed hoppers around shot land, and any gamekeeping practices that involve the use of motorised transport. The closest approximation we could find that did have an established carbon footprint would be commercially reared broiler chickens, as parallels can be drawn between their intensified rearing systems and those that pen-reared pheasants undergo before release (Meluzzi *et al.*, 2008; Meluzzi and Sirri, 2009). However, it is worth noting that this would not take into account the post-release management for pheasants and the possible increases that might cause for pheasant CO2 footprints, but as stated, broiler chickens are the closest analogue we could locate. The CO2 footprint of rearing a broiler chicken under intensive conditions can range from 2.5-8.1kg of CO2 per bird depending on the rearing method (Röös, Sundberg and Hansson, 2014), but a commonly used measurement is 6.9kg (Greeneatz, 2019; Business Insider, 2015). Taking our figure of Enhanced Rearing being used meet harvest rates equivalent to the release of 20 million traditionally reared birds, a reduction in 3.2 million pheasants being reared and released each year (including the additional CO2 from 1% live mealworm to

Enhanced diets) would result in 21.35 million Kg less CO2 being put into the atmosphere each year (Oonincx and de Boer, 2012), equivalent to ~4650 fewer typical passenger vehicles (USEPA, 2017).

As shown in Chapter 2, Enhanced Rearing can lead to an increase in the number of pheasants surviving between years. Although the raw data involved is relatively small, with just 12 Enhanced tags and 4 Control tags counted in the harvest the following year from a total of 2100 of each treatment released, we know from Chapter 5 that these results will be significantly underestimated, possibly by greater than a factor of 10 when Multi-Tags were used, though we are not confident enough in our projections to state a definitive figure. More pheasants surviving between years means that there is likely a larger population surviving into the breeding season, which in itself could lead to more pheasants breeding and further decrease release requirements to meet desired harvest levels. However, pheasant breeding success in the wild is dependent on more than pheasants simply surviving to the breeding season. To accommodate greater breeding populations, management techniques will need to shift towards providing sufficient herbaceous and wood habitat (Leif, 2005), high levels of predator control during the nesting periods (Draycott *et al.*, 2008), and providing supplementary feed beyond the shooting season and into spring (Draycott *et al.*, 2005). Many of these practices are stipulated or encouraged in the Code of Good Shooting Practice (Game and WIldlife Conservation Trust, 2012). Motivating/stimulating such shifts in management would likely be costly and time consuming, and those shoots that have the funds to invest heavily in such pheasant management strategies are usually the commercial shoots. These are the sites where, relative to the high numbers released each year, the small increases in harvest rates caused by increased wild populations and increased year-to-year survival will have little cost-effective benefit, and so the management required to maximise them may be unlikely to be adopted. This means that larger shoots may readily adopt Enhanced Rearing for the immediate benefits it brings to increased harvests of that year, but they may not take full advantage of the benefits it could bring to improving year-to-year survival and increasing wild-bred pheasants. However, shoots that specifically wish to increase the numbers of wild pheasants on their land would likely already be carrying out management practices that could take advantage of the potential benefits Enhanced Rearing brings to improve wild breeding rates.

Our findings regarding tag durability have two broader implications. First, previous studies using Multi-Tags to study population dynamics over a single shooting season post-release (GWCT, unpublished; Turner, 2007) may have reached inaccurate conclusions. Within-site comparisons where tags from the same site are compared to each other, such as those in Chapter 2, should be less affected by this, as tags deterioration rates would be fairly consistent between pens, but for any study where tagged birds are compared to non-tagged birds or absolute tag data is used by itself, tagged birds could be underrepresented by ~14.7%. As discussed in Chapter 5, this can lead to inaccuracies in determining how many immigrant or wild birds are in the harvest, and we have highlighted this using the National Game Marking Scheme as a case study, where overall tag counts are used as a measure of the total release/harvest ratio (GWCT,unpublished). Data and research from the GWCT is often used as a source of information by the UK government when it is seeking advice regarding policy decisions in relation to gamebird management

(GWCT, 2019). By increasing the accuracy of the data that the GWCT can provide, either by deploying our correction factor or using more robust tags, researchers may be better able to inform policy decisions regarding gamebird management nationally. Second, these effects of tag deterioration become more marked for studies of >1 year, and the errors about our correction factor become large and indeed overlap. Therefore, we suggest that researchers interested in gathering data from year-to-year survival should purchase better quality tags. This increase in cost could reduce the number of shoots that tag their birds. However, the resulting data on year-to-year survival of pheasant will be far more robust and allow for more accurate research conclusion and land management that is better tailored to the support the pheasants that are present. Additionally, if shoots are already investing in management specifically designed to encourage year-to-year survival, then the additional cost of a more reliable tag that can better record the efficiency of that management would likely be of little consequence.

Our work at improving the accuracy of aging pheasants using the Proximal Primary Method by adding the mass of the feather to the diameter and length measurements revealed that small improvements could be achieved (1.57% for juveniles and 1.1% for Mature). If the process of gaining the mass value were particularly time consuming, then it might not be worthwhile. Feather drying must always be done to accurately to collect feather length and diameter (Woodburn *et al.*, 2009), but an oven can be used for drying instead of the 12 months of dry storage that we carried out (Woodburn *et al.*, 2009). As such, the additional effort required for the collection of feather mass comes only from the time taken to brush/scrape any excess mud from the feather, place the feather on a set of good quality digital scales, and record the weight, and so we believe that collecting mass data is worthwhile for improving the accuracy of PPM, considering the speed at which the measurement can be taken. Where PPM can be applied most effectively is when the feathers/birds of the smaller known-age subsample can be robustly classified via a broad set of biometrics. This subsample can then be used to calibrate PPM approaches that can be applied to a far larger sample of feathers that can be swiftly collected. Additionally, PPM itself can be used as part of a broader set of biometric classifiers (Woodburn *et al.*, 2009), and so adding feather mass would also likely increase the accuracy of this methods of aging. Our rates of increased accuracy were determined using machine learning, a process that, to the best of our knowledge, has not been used for ageing pheasants before. Despite our rates of accuracy via machine learning being lower than those of previously established method, machine learning may still prove a useful tool for aging pheasants when a broad range of biometrics are added and not just feather metrics, though this would require additional study.

7.3 Limitations of our findings

Even though we did extend the work of Whiteside, Sage, and Madden (2015, 2016) to a commercial rearing setting, our study relied on data from just 8 shoots (2 of which took part in both years), ranging from total releases of 400-10,000. This limited the scope of our investigation, as no very-larger commercial shoots (>10,000 bird releases) were included. This limitation was a matter of necessity. In order for us to carry out Enhanced Rearing, we first had to find a game rearer willing to implement our changes to their rearing practices. Then we had to approach those who purchased their pheasants from that rearer in the hopes that some would be willing to take part in our investigation. To the best of our knowledge, the 10,000 pheasant release was the largest supplied by our game rearer. In the absence of data from very-large shoots, our conclusion that Enhanced Rearing could be as effective on such very-large shoots is inferred from Enhanced Rearing being effective on shoots releasing between 2001-10,000 birds. We believe that Enhanced Rearing will be as effective on such very-large shoots, as those shoots classified as Large within our project invested significant time and resources in their pheasant management in the same manners that very-large shoots do. However, effects such as disease rates from higher density releases (Gethings, Sage and Leather, 2015) or increased rates of predator control from the employment of multiple fulltime gamekeepers many alter the impacts of Enhanced releases on very-large shoots in some way. Without studying Enhanced releases on such very-large shoots, we can only theorise, albeit with some confidence, that Enhanced Rearing would also be as effective upon them.

We also cannot say how many shoots would fall into the Medium category or would release their pheasants too late in the season for Enhanced Rearing to have a beneficial effect. This is because such data on UK shoots simply does not exist. Data from the 2013 Great British Poultry Registry (Animal Health and Veterinary Laboritories Agency, 2013), states that a total of 50,287,533 game birds (primarily pheasants) were kept on ~8111 sites in the UK in 2013, but this covers both releases, rearers, and any other locations keeping more than 50 gamebirds. It gives no further detail on the distribution of the gamebirds amongst those sites or when they were released. The Shoot Benchmark Survey (Game and Wildlife Conservation

Trust, 2018) was carried out over 130 shoots that released a combined total of 1.6 million gamebirds, but again, no data was presented on the distribution of release sizes, and averaging them would put release sizes at ~12,300 gamebirds per shoot, greater than any of our releases in Chapter 2. The average release from our Chapter 2 study was 2040 pheasants across 8 shoots, but in reality only 2 shoots released >2000 birds. Additionally, six of the shoots used in Sage et al's meta-analysis (2018) ranged from 8,000-27,000, the largest release of the sites surveyed in Chapter 4 totalled 60,000, and we know anecdotally of some shoots that release >100,000 pheasants. The GWCT, who are likely the most well-informed body in the world regarding UK pheasant management, also have no truly accurate figures on the number of pheasants releases, the numbers released at each site, or the dates when the pheasants are released (personal comms). Simply put, we do not know definitively where Enhanced Rearing will and will not work. Along with concerns over the rate at which Enhanced Rearing might be adopted, this was the reason for us only applying it to 20 million of the 39-57 million pheasants released each year despite larger shoots accounting for the majority of released pheasants. Another limitation was that, due to the relatively small number of shoots that we released upon, we were not able to investigate if specific management practices would have impacted Enhanced and Control harvests in different manners. Examples of such management practices are; if levels of game cover provided by the shoots varied, would it affect harvests based on differences in dispersal between Enhanced and Control pheasants; if Control pheasants were suffering more from predation than Enhanced, would the type and quantities of predator control alter the numbers of Control birds that survive to contribute to the harvest to a greater degree than Enhanced birds; and are there specific landscape features (e.g. area of woodland, types of crops planted, etc) that have different impacts upon the contribution that Enhanced and Control pheasants make to the harvest? We partially overcame this with the shoot size classification, with those classified as Small, Medium, and Large based on release size also having similar occasional, part-time, and professional game keeping respectively, with gamekeeping effort used as a broad measure for the quantity and quality of overall pheasant management carried out (Sage *et al.*, 2018). If we had been able to increase the number of sites to encompass a broader spectrum of variables relating to harvest sizes, we may have been able to highlight areas where Enhanced Rearing may or may not have worked as effectively. Ideally, we would have been able to experimentally manipulate the types of management each shoot carried out, allowing us to tailor each site for more effective comparisons, but this was simply not possible.

Regarding Chapter 3, we investigated, first, if the flight performance of Enhanced birds differed from Control birds, and second, if flight performance predicted a bird’s likelihood of being shot. Understanding these two points would allow us to, if necessary, add a correction factor to the harvest results to account for any one treatment type being consistently shot at a disproportionate rate. We found that Enhanced birds had consistently higher flight performances and that flight performance affected the likelihood of a bird being shot. However, because the effect of flight performance on likelihood of being shot varied so much over time (high birds were more likely to be shot early in the season whereas they then became the least likely to be shot later in the season), we could not apply a simple ubiquitous correction factors to harvest results. It may have been possible to produce a correction factor that shifted over time, in line with the effect of flight performance on likelihood of being shot, but to do this we would have also required the specific tag counts from each shoot for each shoot-day. However, 4 out of our 8 sites provided only the total tag counts for the entire shooting season, making it impossible to apply such a correction factor to all shoots. Additionally, we would have had to of known if the effects we recorded at the Large class of shoot, where the data was collected from, applied to Medium and Small shoots also.

We could also not differentiate if the change in likelihood of being shot was due to changes in shooting preferences or changes in the ability of those shooting. On smaller shoots, often only one bird is available to be shot at a time, and so there is no ‘picking’ of birds, as every safe bird is shot at, regardless of height. Conversely, on very-large shoots where many more birds are presented to the guns, the rate of ‘picking’ birds might be even higher. Consequently, if we were to repeat the study of the effect of flight performance on likelihood of being shot over a range of shoots that presented varying number of birds to the guns in each flush and the same pattern occurred, this would indicate that the effect was due to a shift in ability and not preference. This would also allow us to determine if different correction factors needed to be applied to different sized shoots.

Our limitations thus far have been in regards to our work regarding pheasants specifically. However, there were also limitations to our invertebrate analysis in Chapter 4 regarding the distances between the exterior pitfall trap transects and the release pens. Additionally, the distance between the traps within the transects themselves was only 5m when other studies recommend 20m (Woodcock, 2005). These two limitations may have caused two effects. First, the close proximity of the exterior transect to the release pen may have caused mixing between interior and exterior invertebrate populations (Melzer and Kaiser, 1988), making any differences between the two locations harder to detect. Second, the close proximity of the individual traps may have resulted in over-trapping of invertebrate populations and reduced total sample sizes (Ward, New and Yen, 2001). However, previous studies have shown that depletion of invertebrate samples in pitfall traps from similar distances to those we carried out were insignificant (Ward, New and Yen, 2001; Baker and Barmuta, 2006). The reason for these limitations was that many of the release pens that we surveyed were small, as were the woodlands within which they were situated (smallest ~2700 m^2). We did not have the space to put greater distance between either the interior and exterior transects or the traps constituting those transects without going outside the woods into very different habitats, primarily that of arable and pasture farmland which have differing invertebrate communities to woodland (Neumann *et al.*, 2015). This limitation was unavoidable given the high number of relatively small release pens and woodlands within which they were located in our study, but as the distances both between transects and the traps within them were kept consistent between all sites, any effects that might have been caused should have been standardised between transect and prevented from producing spurious results. This limitation could have been avoided if alternate sampling techniques had been used, such as vacuum trapping and sweep-net sampling (Doxon, Davis and Fuhlendorf, 2011). However, given the difficulty with which many of the pens were accessed, the distances equipment needed to be carried on foot, and the numbers of surveys required on each site visit, the lightweight and easily mobile nature of the pitfall trapping equipment made the technique very useful for this investigation.

The final limitation that we shall highlight is based on the equipment used as opposed to specific study design, and that limitation is the fact that the patagial tags that we used deteriorate, primarily the Multi-Tags. This limited the data we were able to collect on year-to-year survival for our Enhanced and Control pheasants, and it did so most severely for the birds reared and released in Year 1, as these were tagged with Multi-Tags. However, although this might have affected our between year analyses of annual survival, this limitation did not affect direct comparisons between Enhanced and Control pheasants released in the same year, because both treatments always used the same tag type, so deterioration rates were equal across treatments. To avoid these errors, future studies should use Plastags to mark individuals.

7.4 Future directions for work

7.4.1 Where is releasing Enhanced pheasants most effective?

Several factors that could impact the effectiveness of releasing Enhanced pheasants are worth further study, all of which can be investigated by releasing Enhanced pheasants over a greater number of sites.

First, we found that on Medium releases (601-2000 pheasants) and shoots that released late, Control pheasants actually contributed more to the harvest. While there is a plausible explanation relating to the lateness of release (see Chapter 2), it was not possible to properly separate these two factors within our analysis, as

Medium releases were also typically those that released their bird later. We believe release date had this effect due to later releases not providing enough time for the benefits to survival from Enhanced Rearing to make a significant effect. We theorised that the Mediums shoots may have shot fewer Enhanced birds because they provided less ideal habitat relative the number of birds they release, either preventing Enhanced birds from taking advantage of their improved behaviours and morphologies or increasing their dispersal in search of more ideal roosting habitat. In order to determine if it is later releases, release size, or a combination of both that led to instances of Control pheasants contributing more to the harvest, Enhanced Rearing needs to be tested over a greater number of Mediums sites with varying release dates.

Second, different shoots carry out different types of management. If Enhanced birds are both behaving and surviving differently to traditionally reared birds, the impacts of these management techniques may differ, and these differences must be known in order to maximise the effectiveness of Enhanced Rearing. An example of this would be varying levels of predator control between sites. High levels of predator control have been shown to decrease mortality of pheasant by 29% (Sage *et al.*, 2018), but if Enhanced birds are suffering less from predation, predator control may be less effective. Nest predation rates have also been shown to be significantly lower on sites carrying out predator control (Draycott *et al.*, 2008), resulting in greater breeding success and increased wild populations. This could mean that, in the absence of predator control, increasing the number of pheasants that survive to the breeding season due to Enhanced Rearing may not actually increase the number of wild pheasants if the majority of those surviving birds are predated during the breeding season (Sage et al. 2018). Indeed, where predator control has been carried out extensively for another gamebird species, the grey partridge (*Perdix perdix*), there have been 75% increases in August populations and a 3.5 fold increase in total population in subsequent years due to far more birds surviving to breed (Tapper, Potts and Brockless, 1996). Predator control is just one management technique that could differ between sites. Others include the type and quantity of game cover provided, if supplementary feeding is carried out beyond the shooting season, and reduced pesticide levels to provide more invertebrate food sources for pheasant chicks. By releasing Enhanced birds across many sites with varying management practices and over multiple years, it will be possible to determine which management practices lead to the most benefits to both harvest rates and increasing wild stocks.

Third, we were unable to involve shoots that release very-large numbers of pheasants (>10,000) in our study because our game rearer did not supply to any, yet if Enhanced Rearing were applied to such shoots and achieved the same results as were seen at the Small (<601) and Large (>2000) releases (as we suspect it would), then such very-large shoots offer the greatest opportunity for reducing release numbers. Now that we have shown that Enhanced Rearing is not only effective at increasing harvest rates but also cost-effective, the likelihood of commercial shoots agreeing to participate is higher and offers the opportunity for data to be gathered at the sites where Enhanced Rearing could be most effective.

Rolling Enhanced Rearing out over large numbers of other sites would be a major undertaking, requiring many shoots, multiple game rearers, and likely the backing of an organisation such as the GWCT. However, due to our research the GWCT have already taken aspects of our Enhanced Rearing methodology (namely the provisioning of perching material) and have found a commercial game rearer willing to implement it and shoots wiling to tag their birds and report the results. Using our work as a baseline, such projects can begin to build a far larger dataset than the one gathered during this PhD. With a deeper understanding of where and why Enhanced Rearing can be effective, it could be possible to begin shifting current release practices to adopt it, increasing harvest rates and reducing the need for high density releases.

7.4.2 Can improved roosting behaviours be transferred between Enhanced and Control pheasants?

Chapter 2 highlighted that increases in harvest rates were only present when morphologies associated with increased roosting (increased breast muscle weight and tarsi diameter) were also present. These morphological differences between Enhanced and Control pheasants were absent at the single site where we collected such measures in Year 2, but it appears that, instead of the Enhanced birds failing to develop these morphologies, the Control birds had also developed them in the time between their release and the start of the shooting season. This lack of morphological difference may help explain why we found no difference in harvest rates between treatments at that site that year, as it implies that the Control birds may have developed the roosting behaviours associated with those morphologies. Whiteside, Sage, and Madden (2016) found that by 6 weeks after release, the pheasants that had not been reared with perches were exhibiting night-time roosting behaviours on par with those pheasants that had been given perches, possibly implying that the behaviour could be learnt post-release, as has been seen with improved foraging behaviours in hens and jungle fowl (Nicol, 2004). Our results give more weight to this argument in that the Enhanced pheasants of Year 2 were reared with almost double the perching material of Year 1. By increasing the availability of perching material, the development of natural roosting behaviours in Enhanced birds may have been greater (Heikkilä *et al.*, 2006). If more Enhanced birds were exhibiting increased roosting behaviours in Year 2, it may have led to the Control birds being exposed to greater instances of that behaviour and mimicking the roosting to a greater degree via social learning once in the release pens. Similar adoption of novel behaviours from visual exposure alone have been shown in young chicken regarding pecking stimuli (Suboski and Bartashunas, 1984). If this were the case, then it could have resulted in Control birds developing enough roosting behaviours to increase their survival, producing their equal contribution to the harvest in Year 2. Moreover, the Control birds would have had to develop these behaviours and morphologies to such as degree that by the time they were given access to the outside of the release pens (~4 weeks post-release) and were exposed to predators, their survival rates would already have to closely match those of Enhanced birds. Additionally, the corresponding morphological changes would have had to develop to an equal level by the start of the shooting season (~11 weeks after release), when the first dissections occurred. If this effect of swift knowledge transmission due to increased perching during rearing is occurring, it may only be necessary to rear a proportion of the released pheasants under Enhanced conditions and still achieve the same increases to harvest rate. This could be tested within a controlled environment, as opposed to large-scale pheasant releases for shooting, with groups of pheasants reared with differing levels of perching materials being placed with groups of those reared in the absences of perching material. By monitoring the rate that roosting behaviours were developed by the perch-deprived birds, it would be possible to investigate if providing different quantities of perching material to a sub-population during rearing affected the rate at which perching behaviours were developed by the perch-deprived population.

7.4.3 To what extent do the effects of pheasants on invertebrates differ when invertebrate abundances differ?

Chapter 4 showed a different effect of pheasant releases on invertebrates in release pens in each year of the study, and a key difference between those years was that the overall invertebrate abundance of 2016 was much higher than 2017. When overall abundance was high in 2016, there was lower total invertebrate biomass, slug counts, and detritivore counts within the pen by 4 weeks post-release, with these effects disappearing by 9 weeks post-release. When overall abundance was low in 2017, there was only lower arachnid counts within the release pen by 4 weeks post-release which again disappeared by 9 weeks post-release, but additionally by 9 weeks post-release, the pen interiors had higher total invertebrate biomass, total invertebrate counts, slug counts, and beetle counts. This implies that the effects that pheasants have on invertebrates within the release pen, be they negative in the short term or positive in the longer term, are mediated by overall invertebrate abundance. Further Investigation of this could be important for understanding the wider implications that gamebird releases have on invertebrate communities (Pressland, 2009), and particularly if releases occur in areas where invertebrates of conservation concern are present (Callegari, Bonham and Holloway, 2014).

To investigate this, a range of pitfall transects could be carried out in a similar fashion to Chapter 4 at sites over several years. These would build a dataset of varying overall invertebrate abundances upon which the effects of the release of pheasants can be measured. Additionally, the diet/foraging behaviours of pheasants could be studies to investigate if pheasants that are exposed to fewer invertebrates due to lower invertebrate abundances simply do not develop invertebrate predation behaviours, as such behaviours do increase when young pheasants are exposed to invertebrates during rearing (Whiteside, Sage and Madden, 2015).

7.5 Thesis conclusion

This thesis has further researched and demonstrated a viable method of reducing pheasant release numbers in a cost-effective manner, now within a commercial rearing environment, that does not reduce the number of pheasants harvested. This has pushed forward knowledge regarding the sustainability of the shooting industry environmentally, ethically, and economically. The work we have carried out has laid the groundwork for future studies to continue using our Enhanced Rearing methodology to further refine where it will be most applicable and where it might be improved. We have also investigated potential impacts of releasing Enhanced pheasants, specifically looking at flight performance that is likely of interest to the hunters and effects on invertebrate communities where the birds are released, and found that no additional negative effects arise from the releasing of Enhanced birds when compared to the effects of releasing traditionally reared pheasants. This suggests that the methodology could be widely adopted without fear of detrimental consequences to either the environment that the pheasants are released into or the activity of shooting itself. Such studies of pheasant behaviour and ecology rely on robust methods of data collection. We have refined two such methods. We showed that a widely used patagial tag is not viable for long term data studies and created a correction factor that can be applied to future studies and retrospectively to account for losses of that tag, increasing the accuracy of both past and future datasets and the conclusions drawn from them. We also found a way of improving the accuracy of aging pheasants, allowing for greater certainty in future studies that require pheasants to be separated based on age.

The primary outcome of this thesis is showing that by rearing pheasants under subtly and cheaply enhanced conditions, the birds can be released at lower densities without detrimental effects to shooting yet the same harvest rates could be attained. It is our hope that the outcomes of our research will be used responsibly to reduce the negative effects that large-scale pheasant releases can have on the environment.

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