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Hertfordshire AL4 8AN, UK
www.ufaw.org.uk

Animal Welfare 2020, 29: 1-18
ISSN 0962-7286
doi: 10.7120/09627286.29.1.001

The welfare of game birds destined for release into the wild: a balance between early life care and preparation for future natural hazards

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Abstract

Globally, over 110 million game birds are reared annually and released for recreational hunting. Game birds differ from other reared livestock because they experience two very distinct environments during their lives. Chicks are first reared in captivity for 6–12 weeks under managed, stable conditions and then released into the wild. A limited set of 13 studies have explored how the rearing conditions experienced by chicks influences their pre-release welfare, typically in terms of physical injury (feather-pecking) or behavioural assays of stress responses. However, no studies have considered the specific indicators of welfare of game birds after release. We therefore need to draw from studies that do not specifically investigate welfare but instead ones that examine how rearing environments influence post-release morphology, behaviour and survival. Consequently, we reviewed how reared and wild-born game birds differ and suggest methods by which more naturalistic rearing conditions may be achieved. We noted five areas where artificial rearing deviates substantially from natural conditions: absence of adults; unnatural chick densities; unnatural diet; unnatural physical environment; and exclusion of predation risk. Mimicking or introducing some of these elements in game bird rearing practice could bring two benefits: i) facilitating more natural behaviour by the chicks during rearing; and ii) ensuring that birds after release are better able to cope with natural hazards. Together, these could result in an improved overall welfare for game birds. For example, enrichment of the spatial environment may serve to both improve welfare pre-release and after release into the wild. However, some adaptations may induce poor welfare for a short period in the young birds. For example, exposure to predators may be temporarily stressful, but ultimately such experiences in early life may permit them to better cope with such threats when released into the wild. Therefore, to achieve an optimal welfare for the entirety of a game bird's life, a careful balance between the conditions experienced in early life and adequate preparation for later life in the wild is required.

Keywords: *animal welfare, conservation, hunting, partridge, pheasant, reintroduction biology*

Introduction

People who rear animals have a legal and ethical obligation to ensure good welfare for them (Horgan & Gavinelli 2006; Veissier *et al* 2008; Farm Animal Welfare Council [FAWC] 2009; Grandin 2015). The welfare of an animal is regarded as the state of the individual as it attempts to cope with its environment (Broom 1986) and good welfare is often considered to apply to an animal that is free from hunger and thirst; discomfort; pain, injury and disease; fear and distress; and free to express normal behaviours (FAWC 1993). Good welfare should be sought both during the life of the individual and at their point of death. For most livestock, such as those raised for meat, milk or hides, an individual is farmed under controlled conditions which permits its rearer to continuously monitor and adjust living conditions to ensure high welfare outcomes for the entirety of the animal's life up to their point of slaughter. However, there are other circumstances where rearers only have direct control over an animal for part of their lifespan and this direct care of the animals ceases when they are released into the wild. One situation in which animals reared in captivity are released into the wild is in conservation or reintroduction programmes. A second situation that affects far more individual animals is the rearing of game birds for release for recreational hunting. Whether we can, or indeed should, assess (Kirkwood *et al* 1994) and intervene to improve (Kirkwood & Sainsbury 1996) the welfare of released, free-living wild animals is the subject of debate. However, there is a strong argument that when animals are reared by humans and deliberately released into the wild then we have an obligation to ensure, either through preparatory husbandry or post-release management actions, that they do not suffer from reduced welfare later in life because of our earlier interventions. This argument has been made for reintroductions of species of conservation concern (Harrington *et al* 2013), but the same issues could pertain to the rearing and release of game birds for hunting.

Game birds that are commonly released into the wild (specifically pheasants [*Phasianus colchicus*] and red-legged partridge [*Alectoris rufa*]) are galliformes, like chickens (*Gallus gallus domesticus*), and so it might be assumed that we can simply assess their welfare and advise on their husbandry by copying methods derived for chickens. However, there are two key differences that make us suspect that this may be inappropriate when considering how to assess their welfare. First, game birds are not (intentionally) selected for domestication (Hill & Robertson 1988b; Matheson *et al* 2015). Instead, breeding birds are typically free-living individuals that have survived a shooting season and are caught in the wild before being brought into captivity for egg production. This contrasts with other livestock (including chickens) that have experienced long periods of selection for traits consistent with husbandry and productivity including docility, tameness and gregariousness (Fraser & Broom 1997). Such selection may lead to co-evolved traits that improve welfare outcomes for captive individuals because they are better suited to living in captivity. Therefore, when game birds are in captivity, they will likely respond to stressors in very different ways to those of domesticated chickens. Second, uniquely, game birds are released into the wild when ~6–12 weeks old, where they are free to behave naturally and are not under the direct care of their rearers. After release, game birds face a series of novel, natural threats and must identify and evade predators, navigate their natural landscape, find food, mate and rear offspring (Madden *et al* 2018). The conditions experienced during early life can influence the development of essential characteristics which can influence survival and reproduction (Lindström 1999). Therefore, it is crucial that the welfare and fate of game birds after release should be considered when making recommendations about husbandry pertaining to aspects of welfare during early life. In order to maximise their welfare for the entirety of the game birds' life (both pre- and post-release) we need to understand how husbandry conditions experienced whilst under management early in life prepare them for later life stages when independent. Therefore, we suspect that to maximise the welfare of a reared and released game bird, there needs to be consideration of not just immediate welfare arising from current husbandry practices, but also longer term consequences of such husbandry for the development of appropriate behaviours that ensure good welfare after release.

Each year up to 50 million game birds are artificially reared in Great Britain (PACEC 2008; Great Britain Poultry Register 2013). In France, more than 10 million pheasants and 2.5 million red-legged partridges are reared each year (ONCFS 2013). In the United States, an estimated 10 million pheasants (as well as 37 million quails [*Coturnix coturnix*], 1,000,000 mallards and 200,000 turkeys [*Meleagris gallopavo*]) are reared each year (Burden 2013). In the UK, numbers of game birds reared each year are similar to the total number of domestic chickens reared for egg production, between two and five times greater than the number of turkeys reared for consumption and between 4 and 35% of the annual total of chickens reared for meat production (Great Britain Poultry Register 2013; Defra 2018). Additionally, the number of game birds reared each year is rising. Between 1961 and 2011 there was a 900% increase in pheasants reared in the UK alone (Aebischer 2017; GWCT 2017).

The rearing of game birds, at least in the first few weeks of life, mirrors that of many production animals because rearers have control over the environment. Specifically, on hatching, chicks are typically sprayed with vaccines (eg for Newcastle Disease and Infectious Bronchitis). They are then housed in groups that may range from several hundred to thousands of individuals at an initial density of around 60 birds m^{-2} for the first two weeks of life (Wise 1993; Pennycott *et al* 2012). During this time, they are warmed by artificial heat sources, usually gas brooders, and supplied with high protein, age-specific game feed in excess, as well as water *ad libitum*. The rearing environment keeps the chicks in visual isolation from the outside world. At around three weeks of age (depending on the growth of the chicks and the local weather conditions), chicks are allowed into unheated shelters with grass/stone floors and then on into grass-floored, mesh-walled pens that reduce their stocking density and expose them to less clement environmental conditions including rain and cold, as well as opportunities to view aerial predators. Chicks are often fitted with anti-pecking devices, or bits, which prevent them from damaging one another during aggressive interactions (Butler & Davis 2010). Rearers can utilise veterinary care and administer medication. If disease is detected, antibiotics and anthelmintics can be administered at the flock level.

When pheasants are around seven weeks old and partridges around 12 weeks old, they are released into the wild, an environment that comprises predators, disease, competition and unpredictability. In the UK, once released, they become 'wild birds' under the Wildlife and Countryside Act 1981. Game-keepers will implement management practices to assist game bird establishment post-release. Pheasants are usually released into large, open-topped pens situated in woodland at densities recommended to be no more than 1,000 birds per hectare of pen (Game Conservancy Limited Advisory Group 1990). Such pens are surrounded by fencing to protect the young birds from predators, in particular foxes (*Vulpes vulpes*), while they get used to roosting in trees or mature shrubs (GWCT 1991). The pens contain food and water to entice the released birds to remain in the vicinity. Some breeders clip the wings of the released pheasants to try to reduce the likelihood of their flying out of the release pen during the first few weeks post-release. Partridges are usually released into smaller, enclosed pens set in arable or cover crops which are opened after a few weeks to allow the birds inside to disperse out, having acclimatised to the local environment. In the UK, release is not permitted once shooting has started. After a few weeks, released birds start to disperse out of the immediate area of the pen into the wider countryside. Game-keepers can, and usually do, continue to provide supplementary feed, ensure that water supplies are available, control potential predators and attempt to administer medication (usually via the water supply in the release pen) if they perceive flock-level signs of disease. In addition, game-keepers seek to provide attractive habitats and shelter in order to retain released birds in the area where they will be shot during defined open seasons. Supplementary feeding of released game birds is often ceased at the end of the shooting season (Draycott *et al* 1998, 2005; Hoodless *et al* 1999) but predator control may persist.

We can therefore distinguish two distinct stages of a game bird's life during which it is important to understand how management actions affect welfare: i) when birds are in captivity, during which time direct management and intervention is straightforward, hereafter 'pre-release welfare'; and ii) when the birds have been released into the wild, when direct management and direct care of individuals is difficult, hereafter 'post-release welfare'. Furthermore, we expect carry-over effects between the two life-stages and, therefore, in order to quantify the welfare of a reared and released game bird for the entirety of their life, we need to understand the relative contribution that husbandry makes at each stage and how pre-release husbandry influences, either positively or negatively, the welfare of individuals post-release.

This review will report how studies have assessed welfare of game birds during this rearing period and what is known about how rearing conditions differentially affect welfare. We will not consider the welfare of adult game birds kept for egg production, nor of the welfare implications of management techniques deployed post-release intended to protect, retain and encourage breeding of released game birds. Likewise, we will not consider the welfare of the birds as they are transported or as they are being hunted.

Materials and methods

To discover relevant material we surveyed the academic and grey literature based on queries on Google Scholar and Web of Science. Search terms included: 'game bird(s)', 'Galliform(e)', 'pheasant(s)', 'partridge(s)', '*Phasianus*', '*Perdix*', '*Alectoris*', and their interaction with 'welfare', 'stress', 'mass', 'aggression', 'death', 'mortality', 'survival' also interaction with 'pre-release', 'early development', 'rearing environment', 'post-release', 'in the wild', 'manipulations', 'techniques'. We then followed up references from these first set of papers; only including them in the review if they fitted the search criterion above and if they had been peer-reviewed. Searches were not limited by date. We read each paper and separated them into the following categories: i) assessment of pre-release welfare; ii) assessment of post-release welfare; iii) manipulation to influence pre-release welfare; iv) manipulations to influence post-release welfare; v) any combination of the above. With such paucity of studies, we could not conduct statistical analyses on the data assessed but instead discuss each paper where relevant.

Results

Summary of published work that specifically assesses welfare

With such large numbers of game birds being reared in captivity, it is perhaps surprising that unlike the poultry industry (eg Appleby *et al* 1992; Bessei 2006; Pattison *et al* 2008) there is little research conducted on the welfare of game birds during the early phase of their life in captivity. We encountered only thirteen studies looking at pre-release welfare of game bird chicks and these mainly focused on measures directly relating to productivity (for references, see Table 1). One crude assay of poor welfare is death, particularly if distressed individuals may be more susceptible to disease or infection following injury. However, death may not provide a reliable indicator of welfare because welfare could be poor in individuals that are still alive but has not resulted in their death. We found only a single paper reporting mortality rates in reared pheasants, giving a measure of less than 5% in the first six weeks of life (Đorđević *et al* 2010). If ubiquitous, a 5% mortality level would suggest that annually, around 2.5 million birds in the UK die before release. The remaining studies used more nuanced assessments of welfare based on morphological and behavioural indicators. Eight of these studies focused on levels of feather-pecking and development. Dimmer lighting (Kjær 1997), lower stocking densities (Cain *et al* 1984; Kjær 2004), provision of elevated perching (Santilli & Bagliacca 2017) and provision of a high protein diet (Cain *et al* 1984) all led to a decreased risk of feather-pecking among pheasant chicks, but provision of supplementary amino acids did not alter pecking rates in pheasant or partridge (Madsen 1966). One study explored multiple factors affecting feather-pecking rates in pheasants and determined that provision of fresh green leaf material, the continuous supply of freely available food and low stocking densities all reduced rates of pecking and lower rates were seen in groups of females than in groups of males (Hoffmeyer 1969). Feather-pecking may be accompanied by other negative outcomes and a continuous, as opposed to an intermittent, lighting regime reduced feathering as well as feed conversion and bodyweight (Slaugh *et al* 1990). Feather-pecking can be reduced by fitting anti-pecking devices to birds: adding bits to chicks reduced skin damage from 23% of birds to 3% and halved the occurrence of bird-on-bird pecking, but doubled incidence of head-shaking and scratching and caused nostril inflammation and bill deformities (Butler & Davis 2010). Three other studies used behavioural indicators of welfare. Tonic immobility in galliformes occurs when a short period of physical restraint causes a continued generalised hypotonia after release, based on a natural defence strategy in which remaining still, perhaps mimicking death, dissuades a predator from attacking (Jones 1986). This has been used as an indicator of how fearful pheasants are at the point of capture with more fearful birds remaining motionless for longer once the restraint is removed. No difference was seen in the tonic

Table 1 List of studies focusing on welfare indicators for game birds pre- and post-release.

Species	Stage of life	Welfare indicator	Absence of parents	Unnatural densities	Physical environment	Diet	Predator exposure	Author
Pheasants	Pre-release	Mortality		X		X		Đorđević *et al* (2010)
Pheasants	Pre-release	Growth		X		X		Đorđević *et al* (2010)
Pheasants	Pre-release	Feather damage		X				Kjær (2004)
Pheasants	Pre-release	Feather condition		X				Kjær (2004)
Pheasants	Pre-release	Feather damage			X			Kjær (1997)
Pheasants	Pre-release	Growth			X			Kjær (1997)
Pheasants	Pre-release	Food intake			X			Kjær (1997)
Pheasants	Pre-release	Food conversion		X		X		Cain *et al* (1984)
Pheasants	Pre-release	Growth		X		X		Cain *et al* (1984)
Pheasants	Pre-release	Feather damage		X		X		Cain *et al* (1984)
Pheasants	Pre-release	Feather damage			X			Santilli & Bagliacca (2017)
Pheasants and partridges	Pre-release	Feather damage				X		Madsen (1966)
Pheasants and partridges	Pre-release	Mass gain				X		Madsen (1996)
Pheasants	Pre-release	Feather damage		X	X	X		Hoffmeyer (1969)
Pheasants	Pre-release	Feather development			X			Slaugh *et al* (1990)
Pheasants	Pre-release	Food conversion			X			Slaugh *et al* (1990)
Pheasants	Pre-release	Growth			X			Slaugh *et al* (1990)
Pheasants	Pre-release	Feather condition			X			Butler & Davis (2010)
Pheasants	Pre-release	Mortality			X			Butler & Davis (2010)
Pheasants	Pre-release	Tonic immobility				X		Nowaczewski *et al* (2006)
Pheasants	Pre-release	Blood biomarkers				X		Nowaczewski *et al* (2006)
Pheasants, quail and partridges	Pre-release	Tonic immobility						Nowaczewski *et al* (2012)
Pheasants	Pre-release	Tonic immobility	X					Santilli & Bagliacca (2019)
Pheasants	Pre-release	Dustbathing			X			Vestergaard & Bildsoe (1999)
Pheasants	Post-release	Mortality	X	X	X	X	X	Madden *et al* (2018) (for a review)

immobility of groups of pheasants reared on diets consisting of different vitamin C levels, even though some of these groups differed in corticosterone levels (Nowaczewski *et al* 2006). Tonic immobility levels increased with age within a rearing treatment, suggesting either a developmental process or indicating that the individual was experiencing poorer welfare as they grew older (Nowaczewski *et al* 2012). Tonic immobility was higher in chicks that were artificially reared compared to birds that were reared with foster parents suggesting that they were more fearful (Santilli & Bagliacca 2019). A final study investigated dustbathing, considered to be indicative of positive welfare in poultry (Olsson & Keeling 2005). Restricted early life exposure to dustbaths for reared pheasants reduced their later life dustbathing levels (Vestergaard & Bildsoe 1999). All these studies focused on pre-release welfare, indicated by physical damage or responses in behavioural assays of game bird chicks during the first few weeks of life when under the direct care of rearers. We found no studies explicitly assessing welfare of

https://doi.org/10.7120/09627286.29.1.001 Published online by Cambridge University Press

game birds after release into the wild despite the fact that this period of their life is generally substantially longer than the first few weeks of life spent in the rearing shed. However, there is a review detailing pheasant post-release mortality and the studies that have been conducted to try and improve it (Madden *et al* 2018). Again, survival may not provide a reliable indicator of welfare but any improvements in survival and expressions of natural behaviour are useful indicators of improvement in welfare. We also found little consideration of how artificial rearing conditions affected the expression of natural behaviours in chicks or influenced the development of natural behaviours that are critical for life in the wild after release (but see Vestergaard & Bildsoe 1999 for work on development of dustbathing).

Based on the literature review we identified five broad facets of current artificial rearing and management practices that appear to influence welfare of game birds both during rearing and after release: i) absence of parents; ii) unnatural rearing density and number; iii) physical environment; iv) diet; and v) lack of exposure to predators (see Table 1 to see which papers correspond to each group). In the following section, for each facet, we have made comparisons between the behaviour, growth and fate of wild-born and reared game birds in order to infer how artificial husbandry methods may limit the expression of natural behaviours. We then discuss how the current practice could have implications for pre- and post-release welfare. We finally highlight studies that investigate how manipulations to rearing environments can influence both pre- and post-release welfare. With such paucity of data on game birds we extend the review to include studies on other species that are reared in similar ways.

Absence of adults

Game bird chicks hatched in the wild remain with their mother for an extended period (up to 70–80 days in pheasants [Johnsgard 1999], even longer for grey and red-legged partridges [McGowan *et al* 2013]). Artificially reared game bird chicks are hatched using incubators and reared in large groups without parents in heated houses. The absence of adults during this key period of development is likely to have wide-ranging and profound impacts on pre- and post-release welfare.

Adults warm young chicks. Although precocial, game bird chicks are unable to control their own body temperature immediately after hatching and rely on external sources of heat to thermoregulate. In nature, parents attract chicks to them with specific brooding calls (Collias & Joos 1953). This encourages the chicks to thermoregulate collectively and also standardises periods of activity and inactivity across the brood, influencing the chicks' circadian rhythm (Daan & Aschoff 1982) creating a behaviourally synchronous cohort, further aiding thermoregulation (Lumineau & Guyomarc'h 2000). In domestic chickens, one day old chicks will spend 60% of their time resting under their parent. As feathers develop and chicks are able to thermoregulate, brooding time reduces to around 10% at 13 days old and is absent by 25 days old (Shimmura *et al* 2010). The provision of warmth by parents can be efficiently replicated by game breeders by the provision of heaters. If the rearing house is well insulated, this can provide an even more stable thermal environment than parents and ensure that all chicks can access sufficient heat when required. An even distribution of constant heat will reduce the competition for heat and the stress and injury that can accompany agonistic interactions.

Parental care in early life goes beyond simple provision of warmth. Parent-offspring bonds in game birds are naturally established early on. Prior to hatching, the mother begins to communicate with chicks whilst still inside the egg (Fält 1981). After hatching, adult vocalisation and visual displays are essential aids for chick development. Although the parent does not feed chicks directly, game bird and poultry chicks can socially learn about food. In many galliformes when a parent discovers food, they will emit characteristic high-pitched rapid vocalisations which, along with pecking behaviour, attract the chicks and encourage them to feed (Stokes 1971; Evans 1975; Sherry 1977). In domestic chickens, a feeding display facilitates the acquisition of adaptive foraging skills and knowledge of palatability of food by the chicks (Nicol 2004) promoting the formation of dietary preferences (Wauters *et al* 2002). Furthermore, mothers are sensitive to errors made by the chicks and can emphasise more palatable food items (Nicol & Pope 1996).

An absence of adults can have detrimental implications for pre-release welfare (Napolitano *et al* 2002b). Studies of poultry reveal that the absence of mothers reduces food conversion and growth rate and also increases aggression in growing chicks (Wauters *et al* 2002; Edgar *et al* 2016). Parents have an important role in mediating the chick's response to threats, acting to buffer the stress response of domestic chicks. Chicks reared with access to parents spent more time preening and ground-pecking when presented with a stressful situation (Edgar *et al* 2016) and spent less time being fearful (Campo *et al* 2014) compared with chicks reared with no parents. Rearing with access to parents can also reduce the development of behaviours that directly relate to stress, fear and injury. For instance, an absence of parents in domestic chicks can promote the expression of non-normal feeding and pseudo-sexual behaviours directed towards inappropriate objects and other peers (Le Neindre 1993; Napolitano *et al* 2002a; Riber *et al* 2007). The presence of a parent promotes behavioural cohesion, encouraging individuals of the brood to be either active or inactive at the same time (Daan & Aschoff 1982; Riber *et al* 2007). Lack of behavioural synchrony, as a consequence of constant, uniform heat and light, may cause active birds to disturb and feather-peck resting birds (Gilani *et al* 2012) which can disrupt sleeping patterns, cause injury and be stressful for the recipient. Young pheasants reared with a foster mother showed a lower stress level and a higher response to a simulated aerial predator compared to artificially reared pheasants (Santilli & Bagliacca 2019).

Rearing without access to parents or surrogates can have additional, marked effects on post-release welfare. Released game birds that were reared without parents were not observed performing the behaviours of their parent-reared counterparts. For instance, captive-reared grey partridges exhibited lower individual vigilance levels (Watson *et al* 2007; Rantanen *et al* 2010) and poorer anti-predator behaviour compared with parent-reared partridges (Dowell 1990; Beani & Dessì-Fulgheri 1998). This effect is also observed in a number of avian species reared for release into the wild as part of a translocation programme. Artificially reared houbara bustards (*Chlamydotis undulata*) exhibited poorer anti-predation behaviours compared with birds reared with parents (van Heezik *et al* 1999). Parent-reared whooping cranes (*Grus americana*) were more vigilant and had better foraging ability compared with birds reared without parents (Kreger *et al* 2005). Hawaiian geese (*Branta sandvicensis*) reared without access to parents or foster parents were less vigilant after release compared with parent-reared birds (Marshall & Black 1992). Ultimately, survival after release of game bird chicks reared under surrogate (heterospecific) mothers was better than that of artificially reared birds (Ferretti *et al* 2012), however, surrogate-reared chicks still performed worse than wild-reared chicks (Buner & Schaub 2008), perhaps because inexperienced surrogates may not provide the right cues for chicks.

Even if pre- or post-release welfare could be demonstrably improved by the presence of adults, it may not be a practical solution to implement. Adult game birds are not retained but usually released back into the wild after egg production has ceased. One alternative to using conspecific parents is to use heterospecifics. Historically, before artificial sources of reliable heat were available via gas or electric heat lamps (brooders), game birds were traditionally reared under surrogate poultry parents. This serves well for small-scale game bird rearing operations, but as numbers of reared game birds have increased such surrogacy has become more difficult. Assuming current levels of rearing in the UK (~50 million birds) and that an adult partridge or pheasant can brood 12–15 chicks (Coles 1975), rearing with an adult would require 2.7 million broody hens to be kept in captivity all year round. Alternatively, there are management techniques that can emulate particular actions of adults and so improve pre-release welfare. Brooding (in poultry) can be mimicked by providing chicks with a dark brooder; an artificial source of heat that is fringed with a plastic or rubber perimeter (Stadig *et al* 2018). Chicks use this area to rest, which promotes behavioural synchrony, and it results in the separation of active and inactive chicks therefore reducing the chance that chicks might learn to feather-peck (Jensen *et al* 2006; Gilani *et al* 2012). A switch from continuous lighting to an intermittent lighting regime, perhaps replicating mothers brooding, improved dorsal feathering and feed conversion of pheasants (Slaugh *et al* 1990). Teaching by parents may be replicated by provision of artificial tutors. A motorised arrow used to replicate pecking movements to act as a social stimulus for one day old poultry chicks, resulted in chicks showing a preference for the arrow-pecked stimuli (Bartashunas & Suboski 1984; Suboski & Bartashunas 1984). Puppet-reared Mississippi sandhill cranes (*Grus canadensis*) improved post-release foraging behaviour resulting in survival equal to parent-reared birds (Ellis *et al* 2000). Puppet-reared ravens (*Corvus corax*) were more wary of caretakers and more vigilant prior to release and had better survival after release into the wild, compared with hand-reared birds (Valutis & Marzluff 1999). Puppet-reared takahe (*Porphyrio mantelli*) had equal likelihood of survival compared with wild-reared individuals (Maxwell & Jamieson 1997). Although such investments improve the behaviour of older individuals, they are labour intensive and may not be easy to adopt in large-scale production of game birds. However, given the demonstrable short- and long-term welfare costs of rearing in the absence of adults, we suggest that further work on innovative ways to emulate the developmental opportunities provided by parental care to game bird chicks during early life is an important avenue for research.

Unnatural group size and density of other chicks

In the wild, a brood will consist of 8–13 individuals for pheasants (Johnsgard 1999) and 11–18 for partridges (Potts 2012). In industrial settings, game bird chicks are reared in far larger numbers and at a greater density than naturally reared conspecifics with commercial breeders operating initial densities of ~60 chicks m^{-2}, with up to 1,000 in a single shed (GWCT 1994). Such abnormal social groupings have consequences for pre-release welfare as (in a range of other species) they can induce chronic stress (for a review, see Morgan & Tromborg 2007). Higher density is linked to increased aggression in intensive rearing systems (eg pecking in domestic chickens [Nicol *et al* 1999; Zimmerman *et al* 2006]), and can lead to stress-related changes in blood parameters (eg in captive rock partridge [*Alectoris graeca*] [Özbey & Esen 2007]). Aggression between chicks may arise because of competition for resources, such as food, water or heat, particularly when these can be monopolised (Stahl & Kaumanns 2003). Not only can aggression lead to stress and injury but it can lead to an uneven distribution of resources, with subordinate individuals being hungry, thirsty or cold (Rushen 2003). At extremely high numbers, beyond levels where social structure can be maintained, aggression rates in poultry may actually be lowered (Hughes *et al* 1997) and perhaps an avenue worth investigating in game birds.

The physical effects of aggression may be ameliorated by the application of bits; plastic pieces inserted in the bill. In pheasants, these can halve the rate of bird-on-bird pecking (Butler & Davis 2010) and also reduce the impact of pecking by preventing the beaks from closing so feathers cannot be pulled out. This can improve some pre-release welfare measures. However, the bits themselves may be detrimental to pre-release welfare. Firstly, all birds have to be caught by handlers to have the bit attached and then caught again to have them removed which can induce stress from chasing and handling and increase the possibility of injury. After application, the bits may cause increased head-shaking, scratching, inflammation of the nostril and bill malformation (Butler & Davis 2010). In addition, bits may disrupt the field of view which inhibits learning and behaviour (Ferretti *et al* 2012) and may have longer term consequences on welfare, perhaps influencing the birds after release into the wild.

https://doi.org/10.7120/09627286.29.1.001 Published online by Cambridge University Press

The obvious solution to pre-release welfare concerns caused by high density/numbers is to rear fewer birds or to rear the same numbers but over a larger area. A decrease in stocking density of pheasant chicks from four to 0.7 birds m^{-2} had a beneficial effect on skin condition and plumage quality (Kjær 2004). However, this brings additional economic costs in terms of space and labour. Decreased apparent densities may be achieved in the same floor space by adding refuges or perches, which permit harassed game birds to escape the aggression of others (Cordiner & Savory 2001; Donaldson *et al* 2012; Whiteside *et al* 2016; Santilli & Bagliacca 2017), or sight barriers which served to decrease levels of aggression in adult game birds (Deeming *et al* 2011). These solutions require further exploration. Aggression may also be decreased by making resources harder to monopolise. Bell drinkers, an easily monopolised water dispenser, can be replaced with nipple drinkers which are hard to monopolise; a change which has been shown to reduce aggression in poultry (Zimmerman *et al* 2006; Gilani *et al* 2013). Competition over heat may be moderated by the provision of a dark brooder (Jensen *et al* 2006; Gilani *et al* 2012). The provision of environmental enrichment can result in changes in activity budgets and reduce aggressive pecking as attention is devoted to other activities (Gvaryahu *et al* 1994).

Unnatural densities during early development may have post-release welfare consequences. In salmonids, the stress attributed to overcrowding was believed to be one of the reasons why released fish exhibited inefficient behaviours, such as high general activity and poor habitat choice after they had been released compared to wild fish (Weber & Fausch 2003). The effect that early-life rearing density has on post-release welfare has not yet been explored in game birds and is an area in need of research.

The physical environment experienced during rearing

Game birds naturally nest and subsequently brood in a variety of complex habitats (Haensly *et al* 1987; Rands 1988). On hatching in the wild, precocial game bird chicks, along with their mother, occupy relatively large mean (± SEM) home ranges (grey partridges [first 20 days of life]: 315 [± 41] m^2; red-legged partridges [first 20 days of life]: 457 [± 133] m^2; and pheasants [for first 10 days of life]: 4.5 [± 4] ha [Green 1984; Hill & Robertson 1988b]) and exhibit high dispersal distances (daily movement: grey partridges: 108 [± 19] m; red-legged partridges: 137 [± 22] m; and pheasants: 75 [± 13] m [Green 1984; Hill & Robertson 1988b]) compared to artificially reared chicks which are restricted to the confines of their rearing pens. Therefore, a wild chick will experience a high degree of habitat variation (eg woods, fields, fences and buildings) both in the immediate environment of the nest from where they hatch, and the surrounding areas that their mothers lead them to over subsequent weeks. The ability to orientate and navigate in a complex environment is essential later in life to locate food, mates and shelter. In contrast, artificially reared game birds typically begin life in a barren and spatially simple environment (Buner & Schaub 2008; Hill & Robertson 1988b) of very limited area (some tens of m^2). A barren environment means there are no physical barriers that could cause injury as well as providing clear paths to important resources such as heat, food and water. A barren environment allows the breeder to easily survey the population for injury and disease and maintain cleanliness.

A barren or non-naturalistic environment may detrimentally influence pre-release welfare, particularly if it does not have the features necessary for chicks to perform their natural behavioural repertoire (Clubb & Mason 2003). Prevention from performing these natural behaviours can cause apathy, boredom, frustration and stress across species (Meagher & Mason 2012; Burn 2017) and in poultry increase the expression of damaging behaviours, like fear, feather-pecking, aggression and social withdrawal (Jones 1987, 1996, 2001; Huber-Eicher & Wechsler 1998). A barren and non-naturalistic environment may also compromise pre-release welfare by preventing individuals from escaping attacks by others. Poultry reared without perches or protective cover were subjected to more aggressive interactions compared to birds reared with more naturalistic environments (Olsson & Keeling 2000; Cordiner & Savory 2001; Donaldson *et al* 2012).

Simple manipulations to the early physical environment can improve pre-release welfare. The addition of perching opportunities into the pheasant-rearing environment can lower the density at floor level (Deeming *et al* 2011; Whiteside *et al* 2016) which have density-related welfare benefits (See *Unnatural group size and density of other chicks*). Barriers can distribute birds more evenly throughout the pen which can influence activity budgets in chickens (Ventura *et al* 2012). Providing green material, such as leaves, reduced pecking in pheasants and partridges (Hoffmeyer 1969). Providing dustbaths facilitated increased dustbathing and preening (Olsson & Keeling 2005), a crucial behaviour for game bird welfare.

A barren rearing environment may also cause long-term developmental changes in young game birds that result in poor welfare after release into the wild. Pheasants reared with early access to perches exhibited prolonged bouts of roosting, as well as an increased propensity to roost at night after release into the wild compared to those reared without perches (Whiteside *et al* 2016; Santilli & Bagliacca 2017), culminating in a greater chance of surviving the first eight months in the wild (Whiteside *et al* 2016). Within six weeks there was no difference in the number of pheasants roosting at night between rearing treatments, suggesting that naive birds followed other birds up to roosting sites (Whiteside *et al* 2016). Increased propensity to perch as adults was also observed in chickens that were provisioned with perches as chicks, compared to those reared in barren environments (Newberry *et al* 2001). These behavioural differences are accompanied by differences in morphological development. The addition of elevated perches to rearing sheds allows poultry chicks to increase their bone mineralisation (Reichmann & Connor 1977; Hughes & Appleby 1989), bone mass (Shipov *et al* 2010), bone volume (Hughes *et al* 1993), and bone strength (Fleming *et al*

1994). Pheasants' chicks reared with access to perches grew heavier with thicker tarsal bones compared with chicks reared without access to perches (Whiteside *et al* 2016). A barren environment may also adversely influence neural and psychological development. Poultry exposed to a spatially barren rearing environment had poorer cognitive ability on spatial tasks, such as navigating the environment (Gunnarsson *et al* 2000; Wichman *et al* 2007). Pheasants reared in environments with greater spatial complexity had better spatial working memory compared to birds reared in barren environments (Whiteside *et al* 2016). This may explain why, upon release, reared pheasants do not exhibit the same movement patterns as wild pheasants. Reared pheasants often have greater dispersal distances (Bagliacca *et al* 2010), perhaps as a consequence of poorer navigational and cognitive ability. If this increased wandering arises from them being unable to locate and relocate food sites, then we may expect that such wandering individuals may be stressed and experience reduced welfare.

Introducing perches into commercial game bird-rearing practice is feasible, requiring little additional cost and no change to husbandry routines. Breeders currently rarely provide raised perches, perhaps because it may impede their own movement through the pens, or it may require additional time to install or clean, or simply because they have not considered its benefits. One established risk of raised perches is that birds can collide with them which can result in bone fractures (Gregory & Wilkins 1992). Damage to the keel is particularly prevalent in chickens reared with fixed structures (Wilkins *et al* 2004). However, recent work on modifications to perches, such as the use of ramps, can be used to reduce the effects of keel damage in poultry (Heerkens *et al* 2016) and could be implemented in game bird-rearing systems. The effect that other manipulations to the physical environment, such as to substrates, has on pre- and post-release welfare in game birds has not been studied and should be pursued.

The diet experienced during rearing

In the wild, game bird chicks are omnivorous (Hill & Robertson 1988b). During the first few weeks of life they have an insect-based diet, and after this age they search for more plant-based forage (Dalke 1937; Warner 1979). In captivity, game breeders typically provide commercial chick crumb that is formulated to match the nutritional requirements of the poultry industry. Consequently, the food is monotonous, temporally predictable and presented repeatedly in the same locations (Huntingford 2004; Ferretti *et al* 2012; Homberger *et al* 2014).

Such commercial feeding regimes ensure that birds have the appropriate nutrients *ad libitum*, which facilitates high growth rates and reduces pre-release welfare concerns over starvation. However, the provision of monotonous food in excess and from standardised feeding sites, may mean that the animals have little need to search actively and learn about food (Olla *et al* 1998). Not spending time foraging could have negative consequences during the rearing period if it manifests in spending time conducting undesirable activities such as injurious pecking (Huber-Eicher & Wechsler 1997). Monotony can be overcome by the provision of more natural diet and feeding regimes. In rats (*Rattus norvegicus*), a more complex feeding regime can reduce time engaged in frustration and boredom behaviours (Johnson *et al* 2004). Increased dietary choice *per se* may reduce stress (Manteca *et al* 2008). The provision of live insects or scatter feeding increased the time poultry spends foraging (de Jong *et al* 2005) which may reduce time spent performing detrimental behaviours such as aggression or undirected pacing. The type of feed can improve welfare; chickens that were provisioned with mashed diet had a lower risk of feather damage than those provisioned with pellets (Lambton *et al* 2010).

Diet quantity, quality, type and the way it is presented can influence many morphological, physiological and behavioural characteristics that could have welfare consequences for the birds after they are released into the wild. For instance, captive-reared grey partridge provisioned with a commercial diet grew heavier, had longer small intestines, longer caeca and relatively heavier gizzards than wild conspecifics but with smaller hearts (Putaala & Hissa 1995). Supplementing fibre into the commercial diet resulted in lighter pheasants with longer caeca (Bagliacca *et al* 1993).

Deviations in morphological and physiological characteristics from the wild-reared birds can be assumed to be suboptimal and reduce an individual's ability to cope in the wild. Pheasants reared on commercial chick crumb and released into the wild exhibit poor foraging ability and are unable to maintain body condition when released into the wild (Brittas *et al* 1992; Sage & Robertson 2000). This results in birds developing a high dependence on supplementary feeding which is commonly withdrawn in the spring, resulting in many individual pheasants being unable to make the transition between the supplementary diets and a natural diet (Draycott *et al* 1998; Draycott 2002a). These deficiencies persist into the first breeding season when captive-reared female pheasants rapidly lose condition, resulting in nest abandonment and even death whilst sitting on the nest (Robertson 1997; Hoodless *et al* 1999). An artificial diet may not condition the digestive system to the bulky, more fibrous, and less digestible foods that the birds will encounter after release (Thomas 1987) and the sudden shift to a more natural diet after release will cause birds to lose condition and die if they are unable to assimilate their new forage (Draycott *et al* 1998; Draycott 2002b). However, manipulations to the composition of the diet can help develop physiological characteristics that will improve the survival of released game birds. Grey partridge provisioned with an insect-rich diet during rearing, analogous to the experience of wild chicks, developed primary feathers earlier (Liukkonen-Anttila *et al* 2002), which has been suggested to improve flying ability. Pheasants supplemented with vitamin E during the first week of life increased body size (Orledge *et al* 2012a) and reduced their

https://doi.org/10.7120/09627286.29.1.001 Published online by Cambridge University Press

parasite load as adults (Orledge *et al* 2012b). Pheasants with their chick crumb supplemented with live mealworms and mixed seed were quicker at handling food items and less reliant on supplementary feed after release into the wild. This resulted in the pheasants foraging less, being more vigilant and ultimately showing a greater likelihood of surviving the first year after release into the wild (Whiteside *et al* 2015). In addition, supplemented fibre improved survival of released pheasants (Bagliacca *et al* 1998) and rock partridge (Paganin *et al* 1993) but not for red-legged partridge (Millán *et al* 2003). Pheasant chicks given supplementary protein had improved survival chances in the wild, but only when released into inclement conditions (Scott *et al* 1955). Such survival and welfare consequences are not solely related to the diet of chicks, but also that of their mothers. Hen pheasants fed with supplementary fatty acids produced young with better food-learning ability than hens fed with standardised chick crumb (Bagliacca *et al* 2000). A monotonous food source could have a marked impact on post-release welfare. The provision of an unpredictable food source resulted in grey partridges having a better chance of surviving after release compared to birds with food provided *ad libitum* (Homberger *et al* 2014).

Altering the diet and feeding regime of reared game birds is one aspect of management especially amenable to manipulation and improvement. We suggest that future work explores the effects of altering the form of food and the manner that it is presented when the birds are being reared in captivity on both the immediate growth and development of game bird chicks and how this influences welfare. Encouraging released pheasants to forage (naturally) on native fauna and flora may increase predation pressure on those populations. Consequently, we recommend that wider environmental effects of dietary enhancement are conducted in conjunction with dietary manipulation.

Exposure to predators

Chicks that are reared in the wild immediately share their environment with a number of aerial and terrestrial predators, and so consequently suffer initial high levels of mortality (Hill & Robertson 1988b; Madden *et al* 2018). However, such exposure also provides numerous encounters that do not lead to death but instead stimulate (the development of) appropriate coping, vigilance and escape behaviours. Although some predator responses by galliformes are innate (Göth 2001), other anti-predator behaviour may be learned (Zaccaroni *et al* 2007), and can show a high degree of specificity to particular predator species (Binazzi *et al* 2011). In partridges, following a sighting of a predator, an informed conspecific will give a referential call (Binazzi *et al* 2011) and depending on the call the response of the receiver will differ accordingly. If developing chicks do not experience predators early in life, then they forfeit opportunities to learn (individually or socially) about predator identification and correct responses.

In contrast to wild chicks, artificially reared game birds are protected from predators and rearers use fencing and predator control to ensure that chicks are not disturbed during early life. However, early life naivety of potential threats may prove costly to game birds after release. Artificially reared pheasants and partridges are more vulnerable to predation than matched-weight wild birds (Hessler *et al* 1970; Sage & Robertson 2000), with poor anti-predator behaviour believed to be the reason (Santilli *et al* 2012; Pérez *et al* 2015).

One method of improving anti-predation behaviour is to rear animals in the presence of predators. In fish, this produces individuals less likely to approach model predators and which generally behave more warily (Kelley *et al* 2005; Roberts *et al* 2011). In (non-galliforme) birds, this can be extended by presenting a model predator in association with an appropriate alarm call (McLean *et al* 1999) or witnessing a capture (de Azevedo & Young 2006). In game birds, anti-predator training via the presentation of a predator stimulus in early life influenced vigilance behaviour of captive-reared grey partridge (Beani & Dessì-Fulgheri 1998) and improved post-release survival of released red-legged partridges and chukar (*Alectoris chukar*) (Slaugh *et al* 1992; Gaudioso *et al* 2011). However, even though there is substantial evidence that promoting the learning of anti-predator behaviour can improve the development of important survival skills, inappropriate training may instil incorrect behavioural responses or promote habituation to predators (Starling 1991). For instance, captive rock partridge chicks initially responded to the approach of a dummy predator in a similar manner to naturally reared chicks, with freezing and crouching. However, with subsequent presentations of the predator, the intensity of the response decreased until it was restricted to a simple alarm call without its accompanying crouch and freeze (Thaler 1987). The training process itself may cause anti-predatory responses, such as flight which can increase the risk of colliding with fixed structures within the housing units, resulting possible injury (Gregory & Wilkins 1992). In addition, the confines of the housing units may not allow birds to distance themselves adequately from the stressor which can cause distress.

Clearly, early life exposure to predators or their mimics can potentially bring long-term survival and welfare benefits to captive-reared game birds released into the wild. However, it may be a risky practice and it is not yet known exactly what methods are most appropriate nor what the immediate negative consequences for young game birds may be. We suggest that this area deserves further careful and detailed exploration with particular attention paid to how such methods may be deployed on an industrial scale.

Table 2 A summary of the trade-offs between pre- and post-release welfare for game birds reared under different environments.

		Pre-release	
		Good	*Poor*
		Coincidence of interest (positive)	**Conflict of interest**
		Improves welfare prior to release	Does not adhere to the conditions afforded to the poultry
	Good	Improves development of survival characteristics, eg	Does not adhere to the Five Freedoms
		• Naturalistic diet (Whiteside *et al* 2015) • Perches (Whiteside *et al* 2016; Santilli & Bagliacca 2017); • Foster parents (Ferretti *et al* 2012) • Puppets (Ellis *et al* 2000)	Improves development of survival characteristics, eg • Dummy predator training (Gaudioso *et al* 2011) • Food predictability (Homberger *et al* 2013, 2014)
Post-release		**Conflict of interest**	**Coincidence of interest (negative)**
		Adheres to the conditions of that afforded to poultry	Adhering to the conditions afforded to poultry may not equate to good welfare for game birds
		Adhere to the Five Freedoms	
	Poor	Does not allow for the development of survival; skills, high post-release mortality, eg	Does not allow for the development of survival; skills, high post-release mortality, eg
		Current rearing regime (see text)	Current rearing regime (see text)

Discussion

Determining and improving the welfare of large numbers of game birds reared and released for shooting presents novel challenges that differ substantially from those encountered for other production animals. This is because, although the methods commonly used during rearing result in physically healthy birds under captive conditions, they may not necessarily produce birds that are fully behaviourally, cognitively, physiologically or morphologically developed such that they are adapted to subsequent life in the wild. This problem is not unique to game bird rearers and to some extent mirrors the situation when rearing animals of conservation concern for translocation or reintroduction for which manipulations to the early rearing environment and rearing practice mitigate developmental deficiencies (van Heezik *et al* 1999; Fischer & Lindenmayer 2000; Vickery & Mason 2003; Seddon *et al* 2007), however, the scale for such programmes are often smaller than that facing the game industry. For reintroduction biologists it appears that more naturalistic captive environments provide the greatest opportunity to develop important survival characteristics that will aid a release programme (Shepherdson 1994). However, the natural environment is synonymous with stress, fear and discomfort, all characteristics currently considered tantamount to poor welfare, especially in production and livestock settings. Husbandry that induces low-level stress can be beneficial as some mild stressors can be stimulating, motivating and easily coped with. However, if such stress is overwhelming or chronic, perhaps because of the duration or the valance of the stressor, then it is ultimately detrimental to the individual (Mendl 1999).

Our review of current knowledge on the rearing and welfare of game bird chicks destined for release focuses on the two distinct phases of a game bird's life; the period when the birds are in captivity and the period after they are released into the wild. There is a small set of studies that demonstrate management strategies that may improve welfare during rearing. Even less attention has been paid to the carry-over effects of early-life management in captivity on later welfare outcomes in the wild. Critically, consideration is needed as to how the conditions that chicks experience during the short (few weeks) pre-release period might be balanced against the longer time implications of the welfare experienced in the wild where most birds spend several months. We can envisage four possible scenarios of this balancing act (Table 2)

First, there may be unequivocally negative scenarios in which management that induces poor pre-release welfare also produces game birds that are poorly suited for life post-release. An example here is that an impoverished rearing environment, as a consequence of the barren and non-naturalistic rearing environment currently used in the game-rearing industry, does not allow the birds to express normal behaviours while young which increases apathy, aggression and social withdrawal (Jones 1987, 1996, 2001; Huber-Eicher & Wechsler 1998), indicative of poor pre-release welfare. This same environment may also prevent birds developing the necessary survival skills, causing them to be ill-prepared for life in the wild which could lead to stress, starvation and death; indicative of poor post-release welfare. Such husbandry practices that are detrimental to welfare at all stages should be avoided and alternatives rapidly identified.

The second scenario presents a conflict of interest whereby good pre-release welfare leads to poor welfare of the bird after release into the wild because, although it appears healthy during rearing, it is ill prepared to cope with natural hazards. The current methods of rearing game birds are typically drawn from those developed for poultry. As such, during rearing, game birds receive water, food and warmth when needed. They live in clean conditions, are free from parasites and disease and are treated if signs of illness occur. An obstacle-free environment allows for easy surveying of the animals' state of health and reduces the risk of collisions with obstacles. Wild stressors, such as parasites, disease, predators and unpredictability, are excluded where possible, although stress associated with human contact may occur.

https://doi.org/10.7120/09627286.29.1.001 Published online by Cambridge University Press

Therefore, we can tentatively conclude that, currently, welfare prior to release of game birds is not poor, although studies reviewed here have shown how it could be better. This is supported by observed low mortality (Đorđević *et al* 2010), particularly when compared to their age-matched wild counterparts (Hill & Robertson 1988a; Madden *et al* 2018). However, it seems that when game breeders cosset their captive stock and actively pursue the Five Freedoms (FAWC 1993) during the rearing period, it remains likely that the released individuals are poorly prepared for life in the wild, cope poorly and suffer high mortality rates observed after release. Such management can only be justified in two ways. First, poor preparation for life resulting from excessively clement early-life husbandry can be mitigated once birds have been released by additional management of the post-release environment (killing predators, supplying copious food, administering medication), continuing the dependence of the released game bird on its rearers and keepers. Second, an argument might be made that for short-lived individuals, those which die shortly after release, in order to maximise overall quality of life, it is more important that an individual experiences good welfare for the longer or more important early life stage than for their later (shorter) life after release. However, with > 50% of released game birds surviving to at least the start of the hunting season, a period of > 8 weeks in the wild (Madden *et al* 2018), the majority of game birds spend longer in the wild than they do in captivity.

A third scenario presents a conflict of interest whereby compromises to pre-release welfare improve the welfare of the animal after release into the wild. This may occur when management techniques offer valuable developmental opportunities which incur temporary distress or suffering but which leave the released game birds better able to survive and thrive in a natural environment. An example of this is exposure to (fake) predation attempts during rearing which can promote the learning of anti-predator behaviour (McLean *et al* 1999; Kelley *et al* 2005). This can improve post-release welfare (Slaugh *et al* 1992; Beani & Dessì-Fulgheri 1998) but the presentation of predators, dummy predators or playback alarm calls in captivity can cause fear and distress (Rabin 2003). A second example is the provision of a more naturalistic diet. The natural diet may provoke increased competition and aggression with preferred food items being monopolised (Stahl & Kaumanns 2003), whilst leaving the subordinate individuals hungry (Rushen 2003). However, this diet also promotes the development of foraging behaviour and appropriate gut morphology that can reduce post-release mortality (Whiteside *et al* 2015). Such management practices could be justified if it is considered that the longer time spent in the wild and hence the cumulative welfare experience of an individual outweighs short-term, sub-optimal husbandry and welfare conditions experienced during early life. An additional benefit of improving the survival of released birds up to the point of hunting is that fewer birds need be reared in order to meet the expected harvest levels, and therefore fewer individuals need to suffer the adverse welfare during the rearing period and beyond.

The final, most desirable scenario occurs when early-life management techniques promote both good pre- and post-release welfare. This positive coincidence may occur because offering an environment that promotes natural behaviours during development not only adheres to one of the Five Freedoms, but can reduce pre-release stress (Duncan & Wood-Gush 1972; Cooper *et al* 1996) and can positively impact the long-term physiological, behavioural, neural and immunological developmental processes (McEwen 1999; Suchecki *et al* 2000; Cam *et al* 2003; Salvatierra *et al* 2009; Calandreau *et al* 2011) which can promote welfare and survival post-release. In addition, less-stressed animals often make a better transition to the wild (Teixeira *et al* 2007). For example, the provision of perches in captivity improves pre-release welfare by reducing floor density (Cordiner & Savory 2001), lowering aggression and resultant pecking injuries (Whiteside *et al* 2016; Santilli & Bagliacca 2017) and improving (spatial) cognitive ability (Whiteside *et al* 2016). These positive pre-release effects ultimately improve post-release lifetime welfare by promoting roosting behaviour and reducing the likelihood of predation after release (Whiteside *et al* 2016). A second example; the presence of an adult or experienced conspecific allows chicks to learn important aspects of foraging and predation which improves post-release survival (Dowell 1990; Beani & Dessi-Fulgheri 1998), while also promoting good pre-release welfare by mediating stress (Edgar *et al* 2016) and improving behavioural synchronisation which leads to a reduction in aggression amongst chicks (Daan & Aschoff 1982). Such management is to be recommended and future research that tries to identify interventions that can be applied early in life which improve both current and future welfare outcomes is highly desirable.

Conclusion

The welfare of game birds reared for release for shooting is currently understudied. Most of the post-release research in this review concentrates on mortality, and very little research focuses on specific indicators clearly linked to welfare assessment. Current reliance on examples from the poultry industry risks misunderstanding the requirements and indicators of welfare for game birds. Critically, the welfare of reared game birds should not simply be a product of their early life rearing environment but should also include the conditions that they experience once released into the wild. We have suggested four possible scenarios into which pre- and post-release welfare might be grouped. If there is a conflict between pre- and post-release welfare, then it is necessary to find innovative solutions to balance the two or make a judgement as to whether the short-term welfare costs justify the longer term benefits. Ultimately, the exact balance point between high welfare standards during rearing and after release is one that requires further research. To facilitate this, we first need to identify and validate species-specific indicators of welfare which will allow for the accurate assessment of pre-release welfare of game birds. Secondly, we need to develop appropriate methods of measuring welfare for game birds that have been released into the wild to accurately determine the welfare of game birds after release. This work would differ from conventional research in animal welfare because it demands a move out of the barn or laboratory and into the field where natural conditions may be harder to control and welfare outcomes harder to quantify as animals are less conspicuous for observation and more difficult to sample for physiological markers. Thirdly, a more detailed understanding of the process by which early life conditions influence later life welfare and survival outcomes is required.

Crucially, there is a need to develop management techniques that provide a net improvement in individual welfare across a game bird's lifetime. Such techniques need to be both feasible at an industrial scale and easy to implement by small scale, seasonal game farmers. Some methods, such as rearing under adults or controlled exposure to realistic predatory threat, may not be economically or practically feasible for all breeders. However, if it can be demonstrated that implementing particular management techniques both improves welfare and improves the numbers that are surviving until being shot, then breeders may willingly incur those costs in order to produce birds better able to survive after release into the wild. For these methods, the focus of future research should be on trying to mimic the beneficial aspects of natural rearing processes using synthetic alternatives which may be more affordable, practical and sustainable, such as artificial parents (dark brooders) or predatory stimuli that can be deployed on an industrial scale. Other methods, such as the addition of perches, the provision of diverse diets and implementing feeding enrichments and regimes more similar to those in the wild, already show potential and are likely feasible for immediate implementation by game rearers. What is now required is an understanding of any unintended adverse consequences these methods may impart (for example, improved natural foraging causes a switch from a reliance on supplementary feed to a more natural diet [Whiteside *et al* 2015] which may have detrimental impacts on invertebrate populations, a valuable resource for released game birds or increased dispersal of birds may cause them to leave the estate where they were released thus costing the owner). Integrating these anticipated economic or environmental costs with benefits of improved individual bird welfare can inform how management techniques might best be fine-tuned for particular species or rearing/release conditions. Once established as providing net welfare benefits, such methods should be disseminated widely.

Understanding and attaining a balance between conditions administered pre-release and those experienced post-release for game birds is problematic but vital in order to address and improve the welfare of many millions of individual birds reared each year. It is essential to recognise that game birds differ from poultry and develop appropriate assays of welfare both for game bird chicks during rearing and for birds after release. Most importantly, there needs to be an appreciation that practices intended to improve individual welfare early in life, when rearers can easily observe and manage young game birds, may ultimately have detrimental consequences on lifetime welfare measures. Unintentionally, game bird breeders may cosset their stock but cause them to suffer later in life. Our intention is for this paper to highlight these risks, suggest management strategies to improve game bird welfare, and stimulate future work in this understudied field.

Acknowledgements

MAW and JRM were funded by a European Research Council Consolidator Award (616474) awarded to JRM.

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