The Welfare of Farmed Rabbits in Commercial Production Systems

A scientific review



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Executive summary

Rabbits are the second most frequently farmed species in the EU but are not protected by species-specific legislation. Global rabbit meat production is increasing year on year and reached 1.6 million tonnes in 2014, equivalent to 1.07 billion rabbits. While annual rabbit production in the EU has remained relatively constant over the past 20 to 30 years, France, Italy and Spain together account for 25% of global production. The single largest supplier of rabbit meat to the EU is China.

We identified and reviewed over 600 relevant peer-reviewed scientific articles to assess whether the welfare needs of farmed rabbits are met by the general protection of the Council Directive 98/58/EC that covers all animals kept for farming purposes. Assessing animal welfare requires a collective approach that considers all aspects of their individual experience, as an animal with good welfare by one definition or indicator may have poor welfare by another. We used scientific studies of the natural biology and behaviour of wild rabbits to help inform our review of the standards for farmed rabbits.

The key findings are:-

- Rabbits are one of the most recently domesticated
 mammals and retain many of their wild characteristics.
 Unlike other domesticated species, rabbits have not been
 selected for docile traits, and captive breeding has not
 eliminated their fear of humans. This can be reduced by
 early handling, but selective breeding would provide a
 cheaper (and probably more effective) long-term solution
 to reducing the stress associated with captivity and
 commercial farming.
- Several different rabbit housing systems are used in the EU, but standards vary between countries. Barren wire cages are the main housing system for breeding and fattening rabbits. Some farms have replaced barren cages with enriched cages with a platform and increased cage height, but minimal additional floor space. Only fattening rabbits are housed in groups in cage systems.
- Underground cells are an outdoor system sometimes used in hot climates for individual breeding does, but on a small

- scale. Enriched pens or parks provide more space and enable group housing of breeding does and fatteners, but require more work to clean and manage. Free-range and organic systems remain a small sector, but usually enable grazing and provide access to more space and natural light than is possible in indoor systems.
- Rabbits benefit from social contact, but also choose to spend time alone. High density, contiguous caging systems prevent withdrawal from social contact and may cause sensory overload for rabbits, which rely heavily on olfactory communication.
- Group-housed rabbits exhibit a wider behavioural repertoire: individual housing deprives rabbits of the opportunity to participate in enjoyable social activities such as huddling, resting in physical contact and allogrooming. However, the aggression associated with establishing and maintaining social hierarchies means group-housed rabbits have more injuries and are more stressed. Aggression may be reduced in larger pens or parks that provide sufficient space for subordinates to demonstrate submission. Allowing rabbits to maintain a stable hierarchy will enhance welfare and increase productivity.
- Problems with double littering in group-housed does can be avoided by reducing nest competition: successful methods include doe training and electronic nest box entrances.
- Nest disturbance and the associated kit mortality can be reduced by a suitable nest box design. Nest boxes should encourage normal maternal behaviour by being dark, without an open entrance and positioned a sufficient distance from the main living space to allow does to retreat from kit olfactory and other cues. Doe welfare and kit survival are improved by increasing the separation distance between mothers and kits; sufficient mother-offspring separation is not possible in cage systems either before or after kits emerge from the nest.
- Barren and enriched cages do not provide sufficient space for normal locomotion and vigilance postures and do not allow group housing in does or fattening rabbits since there is insufficient opportunity for conspecific avoidance.

- Fattening rabbits should be housed in groups from weaning, but with sufficient space for conspecific avoidance, especially as they grow, which may involve limiting stocking density. Group size should also be limited to facilitate health monitoring.
- Intense aggression among group-housed bucks precludes social housing in current commercial systems. Large enriched pens several metres in length may provide sufficient space for peaceful group housing, but the potential for group housing bucks in large pens requires further investigation.
- Intensive reproduction on rabbit farms, including an early age of first insemination, high kindling rates and selection for increased litter size and milk production, place unsustainable energetic demands on breeding does, and energy deficits lead to poor body condition, low fertility and high culling rates. Reducing reproduction intensity and the length of lactation improves doe body condition. Weaning at 25-28 days seems to be a suitable compromise between welfare and growth of the kits.
- Wire mesh flooring is uncomfortable for rabbits and causes significant pain and suffering from foot pad injuries. Ulcerative pododermatitis is a leading reason for early culling age in breeding rabbits. Plastic flooring improves rabbit welfare and has productivity benefits for rabbit farmers.
- The low environmental complexity of barren cages
 provides no opportunity for rabbits to perform motivated
 behaviours such as gnawing, hiding and vigilance.
 Providing gnawing objects reduces stress and aggression,
 platforms and hiding places help rabbits cope with
 disturbance, and darker hiding places for resting may
 encourage more natural (nocturnal) circadian rhythms.
- Providing roughage as well as concentrated pellets reduces frustration and stress, and high fibre diets prevent digestive disorders and reduce losses from mortality. A high fibre diet is particularly important in newly-weaned rabbits.

- Loading, transport and lairage are all significant stressors for rabbits and so the time between loading and slaughter needs to be minimised. Selective breeding for docile strains may help reduce the stress associated with loading and transport. Climate control is necessary during transport to minimise thermal stress. The welfare aspects of how rabbits are slaughtered are unclear.
- Welfare standards for rabbit farming vary widely between EU countries, and this leads to confusion by consumers.
 However, since rabbits have specific climatic requirements for good welfare and productivity, different farming systems may be appropriate in different parts of the EU.
- There is a lack of parity in legislation between rabbits and other species farmed in the EU and current legislation does not adequately address the welfare needs of rabbits within existing farmed systems.

Purpose

We reviewed the scientific literature on the biology and behaviour of the European rabbit *(Oryctolagus cuniculus)* in the wild, in the laboratory and in commercial production systems, and used this information to assess the welfare experienced by farmed rabbits. This is essential to conform to the EU Treaty of Amsterdam, which defines animals as sentient beings. We located relevant literature using keyword searches on Web of Science and Google Scholar and identified over 600 relevant, scientifically sound and peer-reviewed articles. Understanding the behavioural needs of rabbits and what they require to be healthy and productive can be used to further develop rabbit farming systems that meet the needs of both rabbits and producers.

Assessing animal welfare

Welfare can be considered by asking two key questions: are the animals healthy, and do they have what they want ^{1,2}? Assessing animal welfare requires a collective approach that considers all aspects of their individual experience, as an animal with good welfare by one definition or indicator may have poor welfare by another.

The Five Domains of Potential Welfare Compromise are nutrition, environment, health, behaviour and mental state 3. These were developed from the Five Freedoms, and outline the key aspects of an animal's experience that influence its wellbeing ³. Animals are considered to have good welfare when their needs in each of these interacting domains are being met. Notably, the domains emphasize the importance of considering mental experiences as well as physical or functional requirements 3-5. In sentient beings, conditions in the nutritional, environmental, health and behavioural domains give rise to emotional experiences, such as pleasure or pain, which determine the animal's conscious subjective experience, or mental state. Combining mental state with conditions in the other four domains culminate in a welfare status that varies along a continuum, from high welfare to extreme suffering.

It is now widely accepted that good welfare is not simply an absence of suffering ⁶. While it is necessary to minimise

negative experiences, it is also important to provide opportunities for positive experiences, as sentient animals are expected to want to minimise pain and maximise pleasure ^{6–10}. Animals are likely to find behaviours such as exploration, foraging and affiliative social interactions rewarding ^{7,11}. When combined with conditions in the other four domains, such positive experiences encourage a positive mental state which, from the animal's point of view, is associated with having a good quality of life ¹², or 'a life worth living' ^{13,14}.

Conditions in the five domains can be assessed using behaviour, e.g. repertoire, activity budget, fearfulness or presence of stereotypical behaviour; or physiology, e.g. heart rate, glucocorticoid concentrations, morbidity or mortality. These measures can be compared between conditions, in behavioural tests, or between captive and wild animals. However, they have to be used with caution, as free-living animals still experience negative mental states and poor welfare due to predation, disease, food shortage and social pressures ².

Choice tests help assess which conditions animals value more ², with those based on the effort they will exert to obtain or avoid each option particularly informative ^{15,16}. The choice itself may be valuable to animals, as choice increases the sense of control, a positive experience that regulates stress responses and contributes to a more positive mental state ^{17,18}.

World rabbit production

Global rabbit meat production is increasing year on year and reached 1.6 million tonnes in 2014, which is equivalent to 1.07 billion rabbits slaughtered in one year ¹⁹.

Compared to the rising trend in the rest of the world, annual rabbit production in the EU has remained relatively constant over the past 20 to 30 years ¹⁹. Between 2005 and 2015, production declined in some EU countries, most notably **France**, **Italy** and **Spain** ²⁰. Data from **Spain** show that per-capita consumption has also declined, and supply has exceeded demand increasingly since 2008 ²⁰. However, France, Italy and Spain remain the top EU producers, and

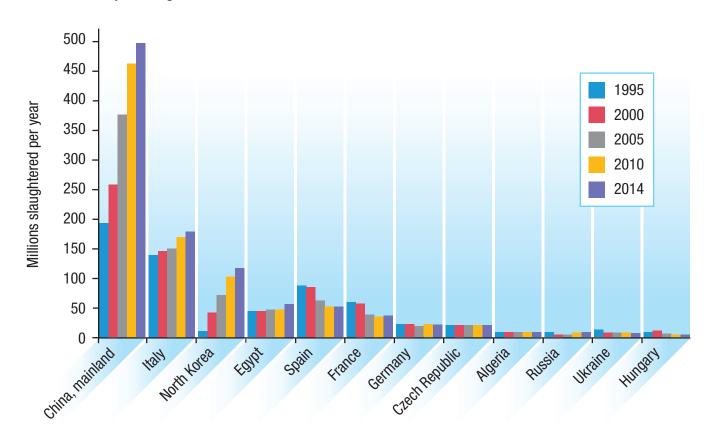
together slaughtered 269.6 million rabbits in 2014 (25% of global production) ¹⁹. Based on total animals slaughtered, rabbits were the second most frequently farmed species in the EU in 2014, after chickens ¹⁹, and so the absence of species-specific legislation is surprising.

International trade of rabbit meat to and from EU countries has declined steadily over the past ten years, with most EU countries trading with each other, rather than with countries outside the EU ¹⁹. However, the single largest supplier of rabbit meat to the EU is China ¹⁹. China is the world's largest producer of rabbit meat and accounted for 49% of global production in 2014, with 499.3 million rabbits slaughtered ¹⁹.

Domestication

Rabbits are one of the most recently domesticated mammals, and domestic rabbits have retained many of the traits of their wild relatives. They were first domesticated in French monasteries ~1400 years ago, when they were bred for meat and began to be selected for size ^{21–23}. From the 16th to the 19th centuries, selective breeding led to increased adult weight ²⁴. More recently rabbits have been selected for increased growth rate, improved feed conversion ratio, larger litter size and reproductive longevity ^{25–29}.

Figure 1. Trends in the number of rabbits slaughtered per year in the 12 highest producing countries in 2014 ¹⁹.



Domestic rabbits have lost the seasonal breeding habits of their wild ancestors ³⁰, and genetic alterations in the nervous system suggest some behavioural adaptation to captivity ³¹, with implications for farms that supplement their stock with wild rabbits without these behavioural adaptations ³². However, 99% of genes are expressed similarly in wild and domestic rabbits ³³, and they still show comparable social, maternal and antipredator behaviours ^{34–40}. So, where relevant, we have used scientific studies of the natural biology and behaviour of wild rabbits to help inform our recommendations for farmed rabbits.

Other domestic species have been selectively bred for tameness, but this has not been done for rabbits, and domestication has failed to eliminate rabbits' fear of humans, which may be perceived as a predator 41 and therefore a significant source of stress in captivity 42-45. Rabbit welfare may be greatly increased by reducing fear of humans, perhaps through selective breeding or early handling 46,47. Exposing kits to humans within 7 days of birth, through gentle handling or exposure to human scent, can significantly reduce human avoidance in both domestic and wild rabbits 44,48-53. Since handling is labour intensive and only successful at reducing fear when done during the critical first week 54, selective breeding may be a more feasible long-term solution ⁴⁷. However, at present rabbits are the only domesticated animals that have not been selectively bred to eliminate the fear of humans.

Rabbit farming systems

Breeding does

- Barren and enriched cages do not permit normal locomotion or sufficient mother-offspring distances
- Underground systems provide a more complex environment but space limitation precludes offspring avoidance after emergence, and there is no social contact with other adults
- Of the main commercial systems, parks are the only one that provides sufficient space to fulfil the social requirements of does, but further modifications (regarding space, nest box design and management) are required to manage aggression
- Selective breeding of rabbits for tameness may enhance the welfare benefits of parks
- Free-range and organic systems remain a niche sector, standards vary between countries and welfare implications are not widely studied

Barren wire cages are the main housing system for breeding does and bucks. Adults are housed alone, and does must share their cage with their kits when they emerge from the nest box, with no opportunity to avoid them. **Enriched cages** are slightly larger, but still designed for single housing. They are enriched with a platform, plastic foot mat and occasionally a gnawing block. Does must share the cage with their kits when they emerge from the nest box, though the platform provides some opportunity to retreat. **Underground cells** are an outdoor system used, on a small scale, in hot climates including **Italy**, Egypt and Vietnam. An underground chamber is connected to an open-air cage by a tube, providing dark areas for resting and nesting, and exposure to sunlight, fresh air and sensory stimulation. Providing a choice of location and thermal environment facilitates thermoregulation 55,56 and may increase a rabbit's sense of control. However, space is limited so does cannot escape their young once they emerge from their nest, enrichment is rare and no direct contact with other adults is possible.

Enriched pens or parks are larger than cages and can accommodate groups of 4-8 does with separate external nest boxes, platforms and often other enrichment items such as plastic tubes and gnawing blocks. Depending on the management, parks may have partitions that allow does to be separated temporarily around parturition. In parks, does can better escape their kits and socialise with other adults. Parks may also incorporate separation areas where only kits can go, which could facilitate the separate feeding of does and kits before weaning. However, aggression can be problematic (see section on Aggression in Social housing, page 12) and parks require more work to manage and keep clean than cages ⁵⁷.

Free-range and organic systems allow access to more space, natural light and (usually) grazing in social groups, but remain a small sector, e.g. in 2016 just 20 farmers raised certified organic rabbits in **France** ⁵⁸. Variable national

requirements for organic production mean standards of welfare differ between countries. For example, on organic farms in **Germany**, rabbits must be kept in groups in enriched runs with indoor and outdoor areas and separate compartments for feeding, resting and socialising ^a, whereas in **Italy** they can still be housed individually and indoor areas may still consist of wire cages with no enrichment ^b. This variation in welfare standards has implications for the awareness of consumers purchasing organic products, suggesting a need for unified organic regulations across the EU.

Examples of farming systems used for breeding does in the EU

	Barren cage	Enriched cage	Underground system	Enriched pens (parks)	Free range & organic
Group housing	No	No	No	Yes, 4-8 does plus kits	Sometimes, group size varies
Floor space, excluding a nest box/platform	Approximately 50x60cm (0.33m²)	Approximately 40x90cm (0.37m²)	Typically 50x60cm outdoor cage with tube to underground cell of 50x50cm (0.53m² total area excluding the nest box)	Approximately 100x200cm (2.32m²)	Varies widely (2.8-1800m²)
Vertical space	30-40cm	60cm	50cm	Open	Open or covered with high net
Substrate	Wire (sometimes with a foot mat)	Wire with a foot mat, or sometimes plastic floor	Plastic underground and grass or wire in outdoor section	Wire or plastic	Grass, with wire/plastic indoor area
Enrichment	None	Platform and sometimes gnawing stick	None	Platform(s) and sometimes gnawing stick(s) and hides	Varies
Natural light	Limited or none in indoor systems	Limited or none in indoor systems	Yes, in outdoor cage	Limited or none in indoor systems	Yes
Nest box	Adjoining the cage, open entrance	Adjoining the cage, open entrance	In underground chamber, open entrance	Adjoining the cage, usually open entrance	Indoors or underground, entrance may be sealable
Able to escape young?	No	Yes, on platform, but not once kits start using it themselves	Yes, in outdoor cage, but not once kits emerge	Yes, on platforms and can move a greater distance from external nest box	Can retreat from visual and probably olfactory range of nest

^a Naturland (2016) Naturland Standards on Production. Verband für ökologischen Landbau. http://www.naturland.de/images/UK/Naturland/Naturland_Standards/ Standards_Producers/Naturland-Standards-on-Production.pdf

b Ministero delle politiche agricole 2012 Norma nazionale per la produzione, preparazione, commercializzazione ed etichettatura del coniglio biologico (art. 42 del Reg. (CE) n. 834/07). URL: https://www.politicheagricole.it/flex/cm/pages/Serve-BLOB.php/L/IT/IDPagina/5880 (accessed 08/01/2017).

Fattening rabbits

- At least 50% of fatteners are still housed in conventional cages, but there is increasing recognition of the importance of space and enrichment for rabbit welfare, leading to a gradual transition to park systems in some countries
- Barren cages, enriched cages and small pens, particularly at high stocking density, do not allow normal resting postures, locomotion or conspecific avoidance
- Outdoor, free-range and organic systems remain a niche sector and their welfare implications are not widely studied

In 2005, conventional **barren cages** were the most common housing system for fattening rabbits in the EU ⁵⁹. Fatteners are housed alone in the smallest cages, or in pairs or groups in slightly larger ones. This allows social behaviour but leads to increasing space restriction as the rabbits grow. **Enriched cages** offer a platform to increase total floor area and have a foot mat and gnawing stick for enrichment, but space restriction remains a problem. However, there is a gradual transition to park systems in **Belgium**, **Germany** and the **Netherlands** ⁶⁰. **Group pens** accommodate larger groups of fattening rabbits. The larger space and open top allows more locomotion and rearing postures, but high stocking densities may negate the benefit of increased space. Enrichment is not always provided in pens. Parks are larger, more structured pens enriched with platforms and gnawing sticks and provide increased environmental complexity in addition to space. Fatteners may also be housed in groups in movable **outdoor** pens, with access to an indoor and outdoor area, or in free range.

Examples of farming systems used for fattening rabbits in the EU

	Barren cage	Enriched cage	Enriched pens (parks)	Free range & organic
Group housing	Usually, groups of 2-9	Usually, groups of 6-14	Yes, groups of 8-54	Yes, group size varies
Stocking density	11-18 rabbits/m² (mean 16)	16-20 rabbits/m ²	12-16 rabbits/m ²	≤1-3 rabbits/m²
Floor space	Approximately 40x70cm (0.28m²) but dimensions vary with group size	Approximately 50x100cm (0.56m²) but dimensions vary with group size	Approximately 100x150cm (1.5m²) but dimensions vary with group size	Varies widely (2.8-1800m²)
Vertical space	30-40cm	70-80cm	Open	Open
Substrate	Wire (sometimes with a foot mat)	Wire with a foot mat, or sometimes plastic floor	Wire, plastic or deep litter	Grass, sometimes with a wire/plastic indoor area
Enrichment	None	Platform and/or gnawing stick	Sometimes platform(s) and/or gnawing stick(s)	Varies; usually at least shelters are provided
Natural light	Limited or none in indoor systems	Limited or none in indoor systems	Limited or none in indoor systems	Yes

What science shows us rabbits need from their environment

Social housing

- Rabbits seek and benefit from social contact, but also choose to spend time alone
- Rabbits must be able to both seek and avoid social contact, including with neighbours in contiguous cages
- High density, contiguous caging systems may cause sensory overload for a species that relies heavily on olfactory communication
- Social support may improve coping ability in captivity
- Stress and aggression can be reduced by reducing fear of humans, perhaps through selective breeding for docile traits

Rabbits are social animals and naturally live in groups of 2-10 animals that share a territory ^{61–66}. Groups normally contain more does than bucks ^{64,67,68}. Rabbits from neighbouring social groups generally avoid each other ^{69–72}, but within groups rabbits are usually within 2-4 metres of a conspecific ⁶³ and sometimes within a body length ^{73,74}, particularly young rabbits ³⁶.

Domestic rabbits are also motivated to seek social contact: in one study, does exerted almost as much effort to access social contact (through a barrier) as to access food, though it was unclear whether the motivation was affiliative or aggressive ⁷⁵. Does paired in cages with access ports to individual cages spent most of their time (up to 88% of observations) in the same cage, and showed little aggression ⁷⁶. Similarly, fatteners select cages with mirrors over those without ⁷⁷, and bucks spent 60% of their time within 15 centimetres of a conspecific, despite having the space to move away ⁷⁸.

Social behaviours in wild rabbits include allogrooming, sniffing and resting in pairs or small groups, often in physical contact ^{39,68,73,79,80}, while they maintain larger inter-individual distances when active. Group-housed domestic rabbits also rest in pairs or trios ³⁹ and spend around 25% of their time in body contact, but mostly when resting ^{78,81}. Rabbits also choose to spend some time alone; in the studies in the previous paragraph, the paired does spent 12% of their time in separate cages ⁷⁶ and the bucks spent 25% of their time apart ⁷⁸. In another study, does offered a choice between solitary and group pens showed either no preference or selected the solitary pen, but not every time, suggesting that pens were selected for the expression of different (solitary and social) behaviours ⁸².

Therefore, rabbits must be able to both seek and avoid social contact in group housing. Small cages or high stocking densities do not allow this choice, often resulting in stress and aggression. Social stress increases heart rate ⁸³ and causes immunosuppressive physiological changes that can be more detrimental to fitness than the physical consequences of fights ⁸⁴. Consequently, efforts to reduce stress and aggression are critical for successful group housing.

Single housing eliminates aggression ⁸⁵, and limiting direct contact with conspecifics also reduces disease transmission ^{86–89}. Single-housed rabbits have indirect social contact with their neighbours, with whom they develop olfactory and visual relationships ^{90–92}, and lie in physical contact through the wire wall ⁹³.

However, single housing provides no opportunity to perform more interactive affiliative social behaviours, such as allogrooming, a key social behaviour observed in wild and group-housed domestic rabbits ^{68,79,94,95}. As single cages are typically contiguous, they also provide no opportunity for rabbits to retreat from unwanted visual or olfactory contact with their neighbours. Rabbits rely heavily on scent to communicate; inguinal (groin gland) secretions are used to recognise conspecifics ^{96–98} and chin marks are used to mark territories ^{99–102} and express dominance ^{100,103,104}. Rabbits may deposit 80-100 chin marks every 10 minutes ¹⁰⁵; they also scent mark with urine and anal gland secretions, which are mainly concentrated at latrines in the wild ^{65,106}. This may contribute to an overwhelming concentration of social odours in high-density housing systems.

Single housing is associated with stereotypical behaviour in does 85 and bucks 78, and in fatteners it increases with age, suggesting a rising level of mental distress from social isolation 81. Stereotypical behaviour is less frequent and develops at a slower rate in pair- and group-housed rabbits, suggesting that stereotypies are either motivated by social deprivation, or that social partners alleviate some of the stress of captivity 81. In wild rabbits, social support reduces fear of predators 63,107 and helps mitigate stress effects on immune function ¹⁰⁸. Rabbits have evolved to live in groups amicably to reduce the risk of predation 107,109,110, which is a key cause of mortality in wild rabbits 111-114 and a significant source of stress ¹¹⁵. The lack of real predators on rabbit farms is often considered to eliminate the need for groups ¹¹⁶. However, humans may be perceived as a threat 41, so the opportunity to seek comfort from social companions may help alleviate stress from human disturbance.

This strengthens the need to reduce fear of humans, as stress and fear can manifest as aggression ^{117,118} and increase injury in group-housed rabbits ⁵¹. The process of domestication usually favours the reduction of aggressive behaviour, coupled with a reduced fear of humans, but domestic rabbits still show a similar level of aggression to their wild ancestors ⁴⁰. However, some genotypes are more aggressive than others ¹¹⁹, or have higher stress responses ¹²⁰, suggesting that fear and aggression could be reduced by genetic selection for more docile traits.

Breeding does

- Doe welfare is improved by opportunities for direct social interactions and the increased space associated with group-housing systems
- Does require sufficient space to establish and maintain stable hierarchies
- Efforts to maintain a stable hierarchy will benefit welfare and increase productivity
- Increasing the distance between nests may reduce aggressive nest defence
- Reducing stress in group-housed does may benefit future generations

- Housing does with a buck reduces pseudopregnancy and increases productivity, but can complicate management
- Training does to recognise their own nest reduces double littering and improves welfare
- Electronic ear tags reduce double littering and improve welfare, but are expensive
- Social disruption caused by semi-group housing systems precludes the maintenance of stable hierarchies and causes unacceptably high levels of stress and injury
- Continuous group-housing provides a more stable social environment than semi-group housing, but modifications are required in current systems to manage aggression more successfully

Opportunities for social interactions, such as allogrooming, mean that group-housed does have wider behavioural repertoires than does housed alone ^{85,93,121}. Groups of does also show less stereotypical behaviour ^{85,121,122}, and spend more time laying stretched out than those in single cages ^{93,123}, suggesting they are more relaxed, perhaps due to a greater ability to escape from their kits ⁹³. This is an important behaviour, as mother-offspring contact is extremely infrequent in the wild; does visit their burrow just once daily to nurse, and generally avoid their kits after they emerge from the nest ^{36,124–126}, presumably to reduce predation risk ¹²⁶.

However, group housing creates problems with aggression involved in the maintenance of social hierarchies. Does in groups have more injuries ⁸⁵ and are more stressed ¹¹⁶, so the welfare benefits of group housing can seem small or unclear in light of the problems that are created ⁹³. This may explain why most breeding rabbits are housed individually ¹²⁷. However, despite being protected from aggression, does housed alone have no means of responding to their isolation, or of resolving conflict with neighbours. This could be considered more detrimental to doe welfare than the possibility of negative social interactions, which occur naturally in the wild.

Aggression

Fight wounds from aggression lead to high culling rates (e.g. 33% ¹²⁸) in group-housed does. Wild rabbits also use agonistic behaviour to establish their social hierarchy, but fighting is generally avoided and attacks are seldom injurious, as rabbits have space to show submission by retreating ^{36,73,80,129}.

As submission has evolved in social mammals to reduce the need for aggressive interactions ^{130,131}, the high injury rates seen in group-housed does suggest that the level of space restriction in current housing systems prevents rabbits from displaying the natural dominance-submission behaviour required to form and maintain stable social groups ¹³², particularly as female aggression also increases with density in the wild ¹³³. This was demonstrated experimentally when pairs of unfamiliar does first introduced in a large pen showed more affiliative behaviour and less aggression during their initial meeting and after separation and regrouping in a smaller enclosure, whereas pairs first introduced in a small pen showed more aggression ¹³⁴.

In wild rabbits, social instability increases stress, aggression and infanticide ^{84,135}. In both wild and domestic rabbits, aggression declines once a stable hierarchy is established ^{84,109,121}, and affiliative behaviours increase ¹²¹. Facilitating the establishment and maintenance of a stable hierarchy could help manage aggression, ideally by maintaining a stable group composition. However, this is problematic when farmers need to replace dead animals ¹³⁶ or does that fail to conceive in synchrony with the rest of the group ^{137,138}. Therefore, efforts to reduce aggression when unfamiliar does are introduced may help them establish stable hierarchies.

Aggression can be reduced by providing sufficient space during introductions, as explained above ¹³⁴. A protected contact introduction period could help check the compatibility between prospective group mates ¹³², particularly if the barrier facilitates scent recognition, since inguinal gland secretions influence the acceptance of individuals into groups ^{96–98}. Reducing fear of humans through early handling also reduces social aggression and contributes to more stable hierarchies ⁵¹. Continual close

monitoring is always necessary to ensure group members remain compatible ¹³².

There is no obvious group composition that minimises aggression. In wild groups, the dominant buck plays a policing role to stop aggressive or sexual encounters between group members ^{36,139}. But grouping does with a buck in captivity does not reduce doe injury rate ¹⁴⁰. Grouping does with littermates may reduce aggression, as wild does maintain stronger social bonds with their female siblings ⁷⁴. However, siblings still fight ^{128,141}.

Rabbits are more aggressive in the breeding season ⁸⁴, and does are particularly aggressive in close proximity to their nest ^{36,68,73,135}. The high aggression among breeding does may be due to natural nest defence behaviour, an adaptation to reduce infanticide ¹³⁵. In the wild, breeding stops (a short tunnel leading to a nesting chamber) are at least 4m apart ¹⁴², and groups are smaller where nest sites are abundant ¹⁴³. Aggression in breeding does is probably elevated by their ongoing breeding status, and further amplified by close proximity nest boxes.

Prenatal stress increases aggressiveness in female offspring ¹³⁸, indicating that reducing social stress in group-housed does could benefit subsequent generations in the short term, and also facilitate selection for reduced aggression.

Pseudopregnancy

Female-female mounting, due to redirected sexual behaviour, is associated with pseudopregnancy (false pregnancy that lasts 16-18 days) ^{144,145}. Pseudopregnancy does not occur in single-housed does but can affect 16% of does when group-housed ¹⁴⁰, and significantly reduces kindling rate (number of litters produced per year) ⁸⁵. Pseudopregnancy can be reduced by housing does with a buck for natural mating, which increases productivity, but also complicates management due to the unpredictable timing of littering ¹⁴⁰. However, this seems a workable solution to reduce pseudopregnancy rates and also facilitates social housing for bucks.

Double littering

Double littering, when two (or more) ¹²⁸ does kindle in the same nest box is fairly common in group-housed does and leads to kit mortality from infanticide. This also occurs in

nature when nest sites are limited, and may help regulate population density ^{74,135}. This density-dependent reproduction ^{73,146,147} has implications for the high stocking densities and close proximity housing used in most rabbit farming systems.

Double littering is undesirable in captivity due to its impact on productivity ¹¹⁶. In two studies, with groups of four does, rates of multiple kindling in the same nest box were 7.7% in a 7.7m² park with a buck ¹¹⁶ and 37.5% in a 4.5m² park with no buck ¹²⁸. The high rate in the latter study could be related to space limitation, and was linked to one nest box being less desirable than the other three, suggesting a need to provide surplus nest boxes to reduce competition.

Does can also be trained to recognise their own individual nest box, which reduces double littering and also stress, indicated by reduced stereotypical behaviour, aggression and injury, and increases positive social interactions ^{85,121}. Alternatively, does can be marked with electronic ear tags that only allow them to access their own nest. Although expensive ¹²⁸, this individual electronic nest box recognition system (IENRS) prevents double littering and infanticide and reduces aggression ⁸⁷, nest disturbance ¹⁴⁸ and kit mortality ¹⁴⁰. The IENRS system also allows does to use their nest box as an undisturbed retreat space once the kits have emerged ¹⁴⁸.

Semi-group housing

An alternative strategy to avoid double littering is semi-group housing, where group-housed does are temporarily isolated in partitioned segments of the group pen from 1-3 days before kindling until 12-18 days post-partum. This reduces double littering significantly, but when does are regrouped aggression is high while the hierarchy is re-established ^{57,149-151}. This frequent destabilisation of the social hierarchy leads to significantly higher rates of aggression and injury compared to does grouped continuously ¹⁵⁰. Studies have reported fight wounds in 16-60% does after regrouping ^{93,122,140,151} and up to 78% if they were grouped with unfamiliar does ⁹³. Consequently, does are usually regrouped with their previous companions to reduce stress ¹⁴⁹. Regrouping or introducing does in a

familiar pen, rather than a neutral one, significantly reduces stress and injury ¹⁵². Enrichment, including platforms and gnawing blocks, also reduces aggression ⁵⁷ in group-housed does.

Management of breeding does

A limited period of aggression may be worth tolerating if the resulting hierarchy allows amicable group living, but if stress and aggression continue, single housing may be more beneficial for welfare ¹³². For breeding does in intensive reproduction systems, repeated isolation and regrouping for each parturition in semi-group housing systems is likely to occur too frequently to facilitate the social stability necessary for amicable group living. Continuous grouphousing provides a more stable social environment than semi-group housing, and is therefore more beneficial for welfare.

As a key behaviour required for the development of rabbit social hierarchies, aggression will never be eliminated from group housing systems, but it could be reduced and managed. A similar situation occurred in domestic breeding sows (female adult pigs), which also underwent a shift from single to group housing in recent years. Like rabbits, sows benefit from the social opportunities and the freedom of movement provided by group housing, and establish their hierarchy by aggression, often at higher intensities than seen in their wild ancestors ¹⁵³. Sows can be group-housed successfully through managing aggression when unfamiliar animals are first introduced. Successful management strategies include gradual familiarisation, providing sufficient space and hiding places. managing competition and maintaining a stable group composition ^{153,154}. In 2013, individual housing of sows was partially banned by EU legislation (Pigs Directive 2008/120/ EC c); the similarity in social behaviour between sows and rabbits suggests that a similar management strategy may be feasible for rabbit does.

^c Council Directive 2008/120/EC of 18 December 2008 laying down minimum standards for the protection of pigs [2008] Official Journal of the European Union L47/5-13. URL: http://eur-lex.europa.eu/legal-content/EN/TXT/?qid=1487548100588euri=CELEX:32008L0120 (accessed 19/02/2017).

Fattening rabbits

- Opportunities for socialisation increase behavioural repertoire and reduce stereotypical behaviour and fear
- Fattening rabbits should be housed in groups from weaning, but with sufficient space for conspecific avoidance, particularly as they grow
- Group size should be limited to facilitate health monitoring
- Stocking density should be limited to prevent social stress and obstruction of movement

Group housing is increasingly being used for fatteners, which are immature and therefore easier to group than adults ¹³², often showing little or no aggression before puberty ¹⁵⁵. However, rabbits reach puberty when around 70 days old ³⁶ and aggression increases ^{141,156,157}, which places an upper limit on slaughter age.

Group-housed fatteners have a more diverse behavioural repertoire compared to single- ¹⁵⁸ and pair-housed ⁹⁵ conspecifics. They are less fearful ^{94,95} and show less or no stereotypical behaviour ^{121,159}.

Health and aggression are less easily monitored in groups larger than 6-8 individuals ¹⁶⁰, yet fatteners are frequently housed in far larger groups, which may impede early diagnosis of ill health. Smaller groups may also be preferable from the animal's point of view; fatteners housed in groups of 8 still rest in pairs or trios ³⁹, and wild rabbits also associate with a limited number of social partners ⁷². Increasing group size may lead to less stable social hierarchies and more frequent aggression ¹⁶¹ and injury, regardless of stocking density ¹⁶². However, the relationship between group size and aggression in fatteners is unclear, as it is often accompanied by a change in stocking density, as larger groups generally require larger enclosures ¹⁶³.

Aggression in groups can be reduced by providing gnawing sticks ¹⁶¹, but it still increases with age ¹⁶¹. This demonstrates the negative effect of increasing space limitation as rabbits grow; in particular, locomotion and time spent laying stretched out declined with age for pairs in cages, but not in

group pens ⁹⁵. Fatteners grouped in cages also acquired ear lesions more frequently than those in pens, due to having to climb over one another ¹⁶⁴.

Decreasing the stocking density improves body condition, promotes exercise and increases playful behaviours, indicating a more positive mental state ¹⁶³. It also reduces aggression ¹⁶⁵, and helps control disease transmission ⁸⁹. However, several studies also report no effect of stocking density on welfare indicators such as fear, aggression, injury rate or mortality ¹⁶³. The optimal stocking density may vary with age, being higher for young rabbits that like to huddle and choose to be together rather than alone 166, but lower as rabbits grow and become more independent 163,166. Reducing stocking density may be beneficial for welfare, since stereotypies can increase when cage size prevents conspecific avoidance 167, and two studies using groups of 8 reported that fatteners were unable to maintain their preferred social distances in pens of 1.5 and 1.6m², a stocking density of 5 rabbits/m² 166,168. However, reducing stocking density reduces farm income, and a study of 15 **Belgian** farms, using small pens, estimated that no profit can be made with a stocking density below 9 rabbits/m² 169. Providing hiding places and gnawing blocks in large pens may reduce the welfare impacts of high stocking density.

Breeding bucks

- Group housing may be possible for bucks, given a suitable enclosure design, but more research is needed
- Current housing systems provide too little space for adequate dominance-submission behaviour by bucks
- Individually-housed bucks may benefit from social contact with neighbours through a barrier, but should be able to seek or avoid this at will

There has been little research into the benefits of group housing for breeding bucks, which are almost always housed singly once they reach maturity at 12 weeks, due to high levels of testosterone-induced aggression ¹²⁷. The minimum

inter-individual distance between wild bucks is 1m ⁷³, and males often exert dominance by chasing 129,170. Small cages or pens are unlikely to provide sufficient space for these behaviours, but experiments with laboratory bucks ¹⁷¹ suggest that group housing may be possible when subordinates have space to retreat several metres, thereby demonstrating an acceptable level of submission to the dominant buck. When the maximum retreat distance was 1.3m, bucks had to be separated after just four hours, but increasing the maximum retreat distance to 6.5m significantly reduced aggression. However, some individuals still had to be separated, indicating that greater retreat distances were required. Group-housed bucks engaged in affiliative and playful behaviours not seen in individuallyhoused bucks, with allogrooming and lying side by side accounting for up to 22% of observed behaviours. This suggests that bucks require and enjoy opportunities to socialise 171.

Reproduction

- Energy deficits in does caused by intensive reproduction lead to low fertility and high culling rates
- Reducing reproduction intensity can be profitable by reducing losses from culling
- Primiparous does require more recovery time before re-mating
- Biostimulation has variable success and the welfare implications for breeding rabbits are currently understudied
- Weaning at 25-28 days seems to be a suitable compromise between welfare and growth
- Efforts to reduce fear of humans through early handling and selective breeding may significantly reduce stress for breeding bucks during invasive procedures
- Nest disturbance is reduced by a suitable nest box design that reduces the detection of kit cues
- Open entrances should be replaced with a cat flap or a tunnel entrance and lidded nest boxes may

- encourage maternal behaviour and natural kit circadian rhythms
- Frustration caused by controlled nursing suggests that this technique is not ideal for doe welfare
- Doe welfare is improved by increasing the mother-young separation distance
- Climatic needs should be considered in housing design: temperature control is required to avoid heat stress in hot countries and cool and damp conditions in more northern and eastern EU countries

Breeding intensity

Farms are intensive or extensive depending on the reproduction rhythm, i.e. the interval between parturition and re-mating. Domestic rabbits do not show seasonal breeding, unlike their wild ancestors ^{172,173}, and rabbit breeders increasingly exploit this by using artificial insemination (AI) in a 33- or 42-day reproduction cycle, and so does are synchronised within groups and often across the entire farm ¹⁵¹.

In **Spain**, 85% of rabbit farms use Al and service 75% of does on day 11 postpartum ¹²⁷. These does produce on average 7-8 litters and 51 kits per year ¹⁷⁴; this is far higher than seen in the wild (approximately 3 litters and 12 kits per season ^{175,176}, due to intra-uterine resorption) ¹⁷⁷, with little or no break between litters to recover energy reserves.

Intensive reproduction may increase the risk of spinal deformities in does ^{137,178}. Concurrent pregnancy and lactation greatly increases energetic demands in both wild and domestic does, but domestic does have been selected for larger litters and their higher energy expenditure is not compensated for by increased feed intake, leading to a loss of body condition and reduced productivity over subsequent cycles ^{179–185}.

Hormonal antagonisms between pregnancy and lactation also interfere with maternal behaviour and reduce fertility ¹⁸⁶. Energy deficits are particularly large in primiparous does, which are first bred between 16 and 21 weeks ^{187–190}, earlier than they would first breed naturally (around 1 year, despite

reaching sexual maturity at 90-125 days ^{36,73}), so are still growing during their first pregnancy and lactation ^{184,191,192}. One study suggested that young does should weigh 4kg at first insemination to optimise litter size ¹⁹³; any earlier and productivity may be compromised by the energy deficit.

Mating does when too young increases culling risk ¹⁹⁰. Low productivity and body condition are the main reasons for short doe lifespans; most does are culled after 6 kindlings (when about 15 months old) ¹⁹⁰, but culling is especially high during the first two pregnancies ¹⁹⁴, highlighting the sensitivity of primiparous does. This contributes to annual replacement rates of up to 120% ¹⁹⁵.

The best way to improve doe welfare is by using a less intensive reproductive rhythm that allows does to maintain a suitable body condition ¹⁹⁵. Increasing the re-mating interval, particularly for primiparous does, reduces doe energy deficits, kit mortality and doe replacement, and increases conception rate 190,192,196-198. These benefits more than compensate for the lower number of kits produced per vear 192,198; an economic analysis found that extensive reproduction with post-weaning insemination ensured a greater financial return than intensive reproduction with insemination 11 days post-partum ¹⁹⁹. However, does on extensive rhythms are at greater risk of obesity, so body condition must be monitored ^{192,195}. Another possibility is to alternate between inseminating one day post-partum and post-weaning, which still reduces loss of body condition significantly and increases productivity ²⁰⁰. In the long term, there is potential for selective breeding for higher feed intake in breeding does to compensate for their high energetic demands 184.

Biostimulation

Farms may use techniques to stimulate ovulation prior to mating to increase fertility and reproductive output. Productivity can be increased by altering the light cycle, nutritional flushing (increasing dietary energy content following a restricted feeding period), brief (24-36h) doelitter separation, a 2-3 day period of controlled nursing or exposure to a buck, all just prior to insemination ^{172,201}.

However, these methods have variable success and have

an impact on kit growth and viability, particularly doe-litter separation ²⁰¹. Also, little attention has been paid to their effect on a doe's mental state: feed restriction, for instance, leads to hunger, and preventing maternal behaviour may be stressful.

Weaning age

In the wild most kits are weaned by day 28 ¹⁷⁷. Many farmers wean rabbits on day 25 to shorten lactation and reduce doe energy requirements ²⁰². This also allows fatteners to be fed a high fibre, low energy diet while their digestive systems are developing: this prevents digestive disorders and reduces mortality ²⁰³. However, weaning earlier than day 25 may increase mortality and reduce growth ²⁰⁴. In **Italy**, organic rabbits must be weaned no earlier than 35 days ²⁰⁵. However, at least in cage systems, weaning after 34-35 days reduces fattener viability ¹⁷⁴ and increases the risk of digestive disorders during fattening ^{206,207} due to prolonged ingestion of the doe's high-energy diet ²⁰⁸ (but see ¹⁸⁷). Late weaning also increases stress by prolonging sucking attempts that does cannot escape, which compromises immune function in does and kits ²⁰⁹.

Semen collection

Semen collection from bucks in Al centres occurs approximately every 12 days and causes significant physiological stress, possibly because bucks are only ever handled during this procedure ²¹⁰. Rabbits can adapt quickly to regular and positive interactions with humans ⁵⁴, but infrequent handling, particularly if associated with an uncomfortable procedure, may increase fear of humans and contribute to chronic stress from continuing human disturbance. Rabbits also distinguish between familiar and unfamiliar handlers ⁴⁸, suggesting that they may associate positive or negative experiences with particular individuals.

Maternal behaviour

Pre-weaning mortality varies from 1-43%, but is usually over 10% ^{211–216}. It is largely a result of poor maternal behaviour, such as a lack of nest building behaviour, kindling outside the nest box, cannibalism or excessive nest disturbance ²¹⁷.

Failure of maternal behaviour may result from an inappropriate nesting environment ²¹⁸, such as unsuitable nesting material ²¹⁹ or nest box design. In the wild, nesting chambers are underground and dark, and kits only leave the burrow at night ²¹⁸. In captivity, nest boxes are exposed to full daylight, which can impede maternal nesting behaviour and cause kits to emerge earlier from the nest ²¹⁸. Lidded nest boxes are darker and provide a more natural environment for both kits and does.

Wild does seal the entrance to their nest with a plug of soil to protect the kits from predators and control when they emerge ¹⁴². Standard nest boxes have permanently open entrances, so does cannot perform this motivated behaviour and are therefore constantly exposed to auditory and olfactory cues from their kits. As does are highly sensitive to these cues and respond by checking their nest 220-222, this increases nest disturbance ²¹⁸ and disrupts the kits' natural circadian rhythm, which is ordinarily determined by the timing of nursing ¹⁸⁸. This leads to excessive cooling and lower sucking efficiency, ultimately increasing kit mortality ²¹⁸. Covering nest box entrances with a cat flap halved the level of nest disturbance by does and significantly reduced nest mortality ²²³. However, nest disturbance still occurred in response to kit odours detected through a cat flap barrier, suggesting that does cannot achieve the feedback associated with successful nest closure when odour is still detectable in small cages ^{221,222}.

Wild does only return to their burrow once a day to nurse, for just 3-4 minutes ^{36,124–126}, and kits have evolved physiological adaptations to this once-daily nursing ¹²⁶. To reduce nest disturbance, some farmers keep nest boxes sealed and only allow does access to their kits once daily. This reduces kit mortality ¹⁷⁴, at least for primiparous does, perhaps by facilitating maternal learning of the natural nursing rhythm ²¹². However, does also show signs of frustration when unable to access their nest at will, at least when housed in cages, as kit cues are detectable ²²⁴.

Larger enclosures facilitate greater mother-nest distances and enable nest modifications, such as tunnel entrances, which better replicate a natural breeding stop and significantly reduce nest disturbance ²²⁵ and litter mortality, even in does that had previously had a complete breeding

failure ²¹⁸. Larger enclosures also facilitate greater mother-young separation after kits emerge from the nest. While platforms allow a doe to maintain some distance from her kits when they first leave the nest, this becomes difficult as the kits grow (see section on Enrichment, page 19) and choice tests indicate this distance is not enough for does, who prefer to spend time in an adjacent cage rather than in the same cage as the nest box.

Climate

Rabbits originated in the Iberian Peninsula and southern France, and are adapted to hot and dry climates ²²⁶. Cooler or wetter conditions significantly reduce reproduction and survival in wild populations ^{113,226–230}. However, heat stress also impairs growth and reproduction and increases mortality ^{231,232}.

Space

- Barren and enriched cages do not provide sufficient space for natural locomotion and conspecific avoidance. This is contrary to Council Directive 98/58/EC which requires that the 'freedom of movement of an animal, having regard to its species and in accordance with established experience and scientific knowledge, must not be restricted in such a way as to cause it unnecessary suffering or injury'
- The slight reduction in slaughter weight associated by increasing floor area seems minor in comparison to the significant welfare benefits
- Barren cages rarely permit natural vigilance postures, in contrast to the Council Directive 98/58/EC requirement for freedom of movement
- Providing a range of cage heights would create microenvironments for rabbits to select for different activities, as they would in the wild
- Rabbits benefit from exposure to natural light, fresh air and mental stimulation
- Outside space is not always feasible, but roof vents or tubes can allow natural light and fresh air into cages, as is mandatory in Austrian rabbit farms

Floor area

Space is a valuable resource: farmed rabbits favour larger spaces in preference tests ²³³ and will work to increase floor area ^{234,235}, particularly during the active period ²³⁵, but also to decrease it, suggesting different sized areas are required for different behaviours ²³⁵.

Rabbits require sufficient floor space for normal resting postures, for efficient sleep, relaxation and thermoregulation: since rabbits cannot sweat ²³¹, they must lie stretched out to dissipate excess heat ²³⁶. When housed in groups, all individuals should be able to lie stretched out simultaneously ²³⁷, which is rarely possible in cages ²³⁸. In a standard barren cage in the EU an average 4.5kg breeding doe uses 19% of the floor area to sit, and 27% to lie stretched out ²³⁸, leaving little room to spare when sharing a cage with up to 10 growing kits. Similarly, at the end of the fattening period a 2.5kg rabbit requires up to 97% of their allotted floor space to sit, and up to 142% to lie stretched out ²³⁸.

Space is required for locomotion. Rabbits move by hopping, jumping and running; in the wild they travel several hundred metres per day 66,239 within home ranges varying from 0.01 to 10 hectares (1000-100,000m²) $^{66,69,133,240-245}$.

Reported distances moved per hop depend on body size and speed, ranging from 15 to 70cm when moving normally ^{78,237}, or up to 1.5m when startled ⁷⁸. So the length of a standard conventional cage barely allows one stride of normal locomotion ^{78,80}. This may explain why captive rabbits spend 50-82% of their time inactive ^{95,155,161,246–254}. Rabbits experiencing long-term space restriction can lose their ability to hop ⁸⁰. Lack of exercise reduces bone thickness ^{137,164,255–257}; breeding does are occasionally culled due to broken bones ^{122,148,190,258} and weak bones may reduce fracture resistance ²⁵⁹ (but see ^{137,256}) and increase susceptibility to osteoporosis and scoliosis ^{80,178}.

Therefore, for good mental and physical health, rabbits need space to perform sequences of normal locomotion: this necessitates a straight line distance of 2-3m for 3-4 hops, and further space for running. Rabbits given more space perform longer hopping sequences ^{164,260} and increase

locomotion ^{94,95,121,155,161,261}, such as jumping and running ^{94,251}, and spend less time inactive ^{161,262,263}. They also perform less stereotypical behaviour ^{167,261,264}, which usually arises from behavioural restriction, so reducing frustration may improve their mental state ²⁶⁵.

From a production perspective, increased exercise can slow weight gain ^{119,155,251,261,266,267} and reduce slaughter weight ^{119,164,255,257,259,261,266–268}. However, reductions may be small, e.g. final weights were 6% lower in 3.36m² pens compared to 0.11m² cages ²⁵⁷, 4.5% lower in 0.95m² barren pens compared to 0.2m² barren cages ¹¹⁹ and 5% lower in 2m² parks compared to 0.38m² enriched cages ⁶⁰.

Vertical space

Rabbits adopt bipedal vigilance postures (rearing) to inspect their surroundings ^{269,270}; vigilance is an important behaviour for prey species and may help rabbits cope with their environment by allowing a greater sense of control ¹⁸. Yet cages are rarely tall enough to accommodate this posture (adults are about 60cm tall). Rabbits rear more when given more vertical space ^{85,121,128,262,271} and, when given a choice, they generally select taller cages, at least during the active period ^{136,272}, and use more enclosed, low-ceilinged areas for resting ^{39,272}.

Outside space

Access to outside space in cages, pens or free-range systems exposes rabbits to natural light, promoting vitamin D synthesis ²⁷³, and provides basking opportunities ^{73,274,275}. Exposure to a wider range of stimuli outdoors also reduces fear of humans ^{276,277} and lowers stress ²⁷⁸, and better ventilation reduces disease prevalence ^{277,279}. Poor ventilation is a problem in rabbit farms, as respiratory disorders are a key cause of mortality ^{127,190,258}.

Substrate

 Wire mesh is uncomfortable and causes significant pain and discomfort from foot pad injuries, in contrast to Council Directive 98/58/EC that requires that 'animals are not caused any unnecessary pain, suffering or injury'

- Plastic flooring is a higher welfare solution than providing plastic foot pads in cages with wire floors and has productivity benefits for farmers
- Bedding provides opportunities for digging and chewing to reduce boredom, and increases locomotion, but requires regular replacement to control bacterial growth

Wild rabbits spend most of their time on solid, soft substrates such as soil, sand and grass. In captivity, floors are usually slatted or perforated for ease of cleaning, and hard.

Wire

Most cages have wire mesh floors to prevent the accumulation of urine and faeces. However, wire mesh damages footpads and can lead to significant discomfort from ulcerative pododermatitis (sore hocks). This is a common problem in breeding rabbits and affects up to 72% of does housed on wire floors ²⁸⁰. In severe cases animals must be culled, contributing to the high annual replacement rates seen in breeding does (60-120%) ^{85,195,199,200,206,281,282}. While some legislation, e.g. in the **Netherlands**, specifies a minimum wire thickness, thicker wire does not reduce the incidence of footpad injury ²⁸³.

Plastic

The most common alternative to wire is perforated plastic flooring, or covering part of the wire with a plastic foot mat. Foot mats are now widely used on farms in the EU to alleviate footpad problems caused by constant contact with wire ²⁸⁴. Plastic foot mats and flooring can help prevent and cure footpad problems ^{42,137,213,280,284–287} and improve overall body condition ²⁸⁶ in breeding does.

However, because rabbits with foot mats still use the wire areas of their cage, and even minimal contact with wire causes foot pad lesions ^{137,280}, plastic floors are preferable to foot mats for rabbit welfare. Evidence from both breeding and fattening rabbits suggests plastic flooring is more comfortable and preferable to wire ^{161,288–290}. Plastic flooring also has productivity benefits ¹³⁷, with higher weight gain and/or slaughter weight on plastic floors compared to wire ^{289,291} or wooden slatted floors ¹⁶⁵.

Bedding

Bedding has welfare benefits by increasing locomotion ¹⁵⁵ and providing digging and chewing opportunities to reduce boredom ²⁹². However, it is imperative to keep bedding materials dry by replacing them regularly, as damp material harbours bacteria and can increase mortality ^{88,155} (but see ²⁵³). Rabbits also avoid damp bedding ^{253,291,293}, and damp substrates such as wooden slatted floors ²⁹⁰. The labour costs involved in replacing bedding regularly to keep it clean and dry means that few farms provide it continuously.

Enrichment

- Gnawing objects reduce stress and aggression, but multiple objects must be provided in group housing to prevent competition
- Platforms improve welfare by enabling vigilance, hiding and mother-offspring separation, but multiple platforms are required to reduce competition
- Plastic platforms are better for welfare, as wire causes foot pad injury
- Hiding places aid conspecific avoidance to reduce stress and injury, and may facilitate coping
- Darker hiding places for resting may encourage more natural circadian rhythms
- Enrichment possibilities are limited by space, supporting the need for larger enclosures to facilitate increased environmental complexity
- When enriched pens are large enough to provide different microenvironments, rabbits use different areas of the pen for different behaviours; this natural behaviour is not possible in barren or enriched cages

Gnawing sticks

Food intake in rabbits is controlled by the behavioural need to chew, as well as by hunger ²⁹⁴, and they may direct chewing behaviour towards the cage or conspecifics when unable to fulfil this motivation. Gnawing materials direct chewing towards more appropriate materials ²⁹⁵, thereby reducing oral stereotypies ^{296–298} (but see ^{247,299}) and conspecific aggression ^{57,161,268,297}. However, it is important

to provide multiple gnawing objects in group housing to limit competition, which can increase aggression ³⁰⁰. Gnawing opportunities also reduce inactivity and restlessness, which can indicate stress ^{161,249,301}. The presentation method influences the welfare benefit of gnawing sticks, e.g. hanging sticks can be more difficult to manipulate than sticks attached to the wall ²²⁴. Given a choice, rabbits prefer cages with gnawing sticks than without, suggesting that they are a valuable resource ¹⁶¹.

Platforms

Rabbits are more motivated to gain access to a cage with a platform than one without ⁷⁵, and spend a significant proportion of their time (up to 40%) on a platform, suggesting that they are a valuable resource ^{288,302}.

Platforms significantly increase locomotor activity by providing more floor space and opportunities for movement 302, without reducing performance 43,251. Rabbits use platforms to gain a better view of their surroundings, but also to shelter underneath 271,303. Platforms enable lactating does to escape from their young 42,225,288; this may lower stress and reduce loss of condition during lactation 304. However, more than one platform may be required; does have no means to escape once kits grow large enough to use the platform themselves 42, and fattening rabbits use platforms less as they grow due to competition for space 43. As with the cage floor, wire platforms can contribute to foot pad lesions, so plastic surfaces are preferable 42.

Hiding places

Wild rabbits graze within easy reach of a refuge ^{241,305,306}, so hiding places in captivity may facilitate coping during periods of disturbance. Rabbits seek shelter under platforms or other enrichment structures more often when disturbance is high ^{42,43,251}, and hiding places enable conspecific avoidance ^{168,296}, which reduces aggression ³⁰⁷, stress ^{271,308} and injury ¹²².

Rabbits mainly feed at night and rest under cover during the day ^{172,245,309}. When given a choice, does select darker cages during the day ³¹⁰, and wild rabbits also prefer darker, more enclosed warrens ³¹¹, suggesting that hiding places that

block out the light for daytime resting may facilitate rabbits' nocturnal circadian rhythm ^{172,245,309,312,313}.

Nutrition

- Roughage promotes longer chew times than concentrated pellets, and reduces frustration and stress
- Hay increases water intake: this prevents calcium accumulation and reduces cleaning labour
- High fibre diets prevent digestive disorders and reduce losses from mortality
- Improving gut health by increasing dietary fibre may improve digestive efficiency
- A high fibre diet is particularly important for healthy gut development in newly-weaned rabbits

In the wild, rabbits spend 14-19% of their time feeding on fibrous, low energy herbaceous grasses and cereals and gnaw on branches, roots and bark ^{79,80,309,314,315}. The concentrated pellet diet of most farmed rabbits requires less time to consume, leaving time to fill, and boredom ³⁰⁹. Roughage such as hay encourages longer periods of chewing, reducing inactivity ^{316–318} and stereotypical behaviour ^{299,317–319} (but see ²⁹⁹). Providing hay ¹¹⁹, but not straw ¹²², may also reduce aggression.

On organic farms in **Italy**, plant material must comprise at least 15% of the daily diet ²⁰⁵. Fatteners generally select grass or hay over pellets ²⁶¹, though they do not work harder to access grass than commercial feed ³²⁰. Farmers may be reluctant to provide hay, as increasing dietary fibre reduces total energy consumption and slows growth ¹¹⁹. However, hay also increases meat tenderness ²⁵⁵, and water intake, which can prevent calcium accumulation, with advantages both for urolithiasis prophylaxis and reducing cage cleaning labour from urine residues ^{321,322}.

Wild rabbits balance their nutritional intake by adapting their intake rate and feeding on a wide range of plant species ^{84,314,315}. Providing roughage may allow domestic rabbits to regulate their own nutritional intake.

Digestive disorders due to inappropriate nutrition, often coupled with poor hygiene and high stocking densities, are the leading cause of morbidity and mortality in fattening and breeding rabbits 127,323-326. As herbivores, rabbits have specific fibre and protein requirements to regulate their gut flora and the rate of feed passage. Low fibre diets increase morbidity and mortality from digestive disorders ^{327–333}, but increasing fibre dilutes digestible energy and can impair growth 328,332,334,335. However, fibre may also improve digestive efficiency by promoting better gut health ^{327,331}. Finding the balance between high fibre for digestive health and high starch for growth is a key problem in fattener nutrition ^{335,336} but, despite reducing growth rates, high fibre diets are highly beneficial for both welfare and production. as preventing enteropathies and mortality reduces both suffering and financial losses.

In young rabbits, fibre deficiency impairs the development of microbial gut activity ³³⁷. The fibre:starch ratio is particularly important in the two weeks post-weaning, while the digestive system is still developing 338 and fattening morbidity and mortality are highest ^{203,324}. In **France**, 90% of rabbit breeders use short-term feed restriction (80% of ad libitum) at this time to reduce digestive disorders; despite leading to hunger, this significantly reduces morbidity and mortality due to enteric disorders ³³⁹. Another possibility is feeding separate diets to does and kits before weaning, using weighted grills, to reduce kits' intake of their mother's high energy diet; young rabbits fed a high fibre/low starch diet around weaning generally have better digestive health. but effects on growth are mixed 338 and preventing access to the mother's diet does not always reduce kit morbidity or mortality ²¹⁶.

Handling, transport and slaughter

- Loading, transport and lairage are all significant stressors for rabbits, and better welfare is achieved by minimising the time between loading and slaughter
- Reducing fear of humans may reduce stress during loading and transport

- Distances between farms and abattoirs should be short to minimise journey times
- Climate control is required during loading, transport and lairage to prevent thermal stress
- Managing the total duration of fasting requires careful coordination between farm and abattoir personnel, which may not be easy to achieve
- Access to water may lessen the welfare impacts of fasting
- The welfare aspects of how rabbits are slaughtered are unclear

Conditions, handling and time during loading, transport, lairage and slaughter have clear impacts on fattener welfare, and better welfare is achieved by minimising the time between loading and slaughter ³⁴⁰.

Loading

Trauma during loading increases the risk of injury 341 and mortality 342 . Gentler handling during loading does not reduce transport stress 343 , suggesting that reducing aversion to handling by reducing fear of humans may be the only way to reduce loading trauma.

Transport

Transport is highly stressful for rabbits $^{340,343-345}$, even after just 30 minutes 308 , and the risks of bruising 346 and transport mortality 346 increase with journey duration. In Europe, journeys from farm to abattoir last up to 4 hours 165,255 , and may include stops to collect rabbits from different farms, increasing the time spent in the lorry 347 .

Rabbits are usually transported in barren crates containing 6-16 individuals and stacked on average 6 tiers high, amounting to 1500-6000 rabbits per load ^{342,343,347}. Rabbits on the bottom tier have higher stress levels and are subject to falling excrement through perforated floors ³⁴⁸; solid floors may prevent this ³⁴⁰ but hinder ventilation ³⁴². Crates stacked at high density, coupled with a lack of temperature control on most transport lorries, means that

ventilation can be poor, particularly during stops, putting rabbits at risk of thermal stress ³⁴². Heat stress has a detrimental impact on rabbit welfare during transport ^{346,349,350}. To reduce heat stress, journeys may be timed to avoid the hottest part of the day ^{345–347}, but more reliable means of climate control are required.

Fasting

Food and water deprivation is detrimental to welfare, yet rabbits are fasted from loading to slaughter to reduce faecal contamination. This leads to hunger, thirst and weight loss, primarily from gut emptying ^{345,351}, but also depletion of energy reserves when fasting exceeds 6-9 hours ^{341,352}. Providing water before transport can reduce weight loss ^{340,353,354}, but does not alleviate hunger or the behavioural need to chew. Fasting durations can be shortened by minimising journey times, but it is also important to consider the duration of loading (~90 minutes) ³⁴⁷, unloading (~23 minutes) ³⁴⁷ and lairage (~2 hours, but sometimes up to 7 hours) ³⁴⁷.

Lairage

Lairage allows rabbits time to recover from transport, mainly to improve meat quality, but may also reduce slaughter stress ^{340,348}. However, holding areas rarely have food, water or temperature control ³⁴⁷, and longer lairage increases pre-slaughter mortality ³⁴⁶. Some abattoirs hold caged rabbits within visual, auditory and olfactory range of the stunning area, and this may cause significant distress to the animals prior to slaughter ³⁴⁷.

Slaughter

At slaughter, rabbits are electrically stunned and then bled out 255 . Gas stunning is not recommended as it causes a significant period of discomfort before taking effect 355 , and rabbits have a naturally high tolerance to CO_2 (carbon dioxide) 356 .

However, rabbits may also experience unnecessary suffering during electrical stunning if the voltage is too low ³⁵⁷ or when electrodes are positioned incorrectly; in one study this happened on 10.8% of stunning attempts ³⁵⁸.

Some individuals may also fail to be stunned by one or more attempts, regardless of voltage or electrode position ^{357,358}, or return to sensibility before being slaughtered ³⁵⁸. Pain perception is difficult to identify in prey species that typically show less overt signs of pain, so it is still uncertain whether pain is truly absent after 'successful' electrical stunning ^{359,360}.

Standards for commercial rabbit farms in the EU

Despite being the second most frequently farmed species in the EU, in terms of numbers, there is no species-specific legislation to safeguard the welfare of farmed rabbits. They are only given general protection, under the Council Directive (98/58/EC) concerning the protection of animals kept for farming purposes d, the Council Regulation (EC No 1/2005) on the protection of animals during transport and related operations e and the Council Regulation (EC 1099/2009) on the protection of animals at the time of killing f. Since the standards of the General Directive are lower than the standards of species-specific directives for other livestock, such as calves, chickens and pigs, the General Directive is unlikely to enforce an acceptable level of welfare for rabbits. Not only is there a lack of parity in legislation between rabbits and other species but, as we have shown in this review, current legislation does not adequately meet the welfare needs of rabbits within existing farmed systems.

There is an urgent need to introduce specific legislation for rabbits that recognises their particular requirements and specifies the farming systems that promote acceptable levels of welfare. Several EU member states and other European countries have already recognised the lack of protection afforded to rabbits and implemented national species-specific legislation. Barren cages are now banned for breeding does and fattening rabbits in **Austria**, **Belgium**, **Germany**, the **Netherlands** and Switzerland. **Belgium** ⁹ has also banned enriched cages: all new systems built for fattening rabbits must be roofless parks, and all breeding does must be housed in parks by 2021.

In **Austria** ^h, enclosures must have exposure to natural light, roughage, gnawing material and a platform. In **Germany** ⁱ, breeding and fattening rabbits must have a platform, gnawing material and roughage. In the **Netherlands** ^j, fattening rabbits must be housed in pairs with a platform and gnawing material. In Switzerland ^k, cage size and platform size requirements increase with animal weight: cages must include a dark hiding area, gnawing objects and roughage, and fatteners must be housed in groups.

However, in most of the EU conventional caging remains a legal and popular farming system for rabbits. Since rabbits are the second most frequently farmed animal in the EU, with **France**, **Italy** and **Spain** alone slaughtering 269.6 million rabbits in 2014 (25% of global production), an integrated approach is needed to ensure adequate welfare across the Union.

- ^d Council Directive 98/58/EC of 20 July 1998 concerning the protection of animals kept for farming purposes [1998] Official Journal of the European Communities L221/23-27. URL: http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX%3A31998L0058 (accessed 08/01/2017).
- Council Regulation (EC) No 1/2005 of 22 December 2004 on the protection of animals during transport and related operations and amending Directives 64/432/EEC and 93/119/EC and Regulation (EC) No 1255/97 [2005] Official Journal of the European Union L3/1-44. URL: http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32005R0001 (accessed 08/01/2017).
- [†] Council Regulation (EC) 1009/2009 of 24 September 2009 on the protection of animals at the time of killing [2009] Official Journal of the European Union L303/1-30. URL: http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX%3A32009R1099 (accessed 08/01/2017).
- ⁹ Belgian Royal Decree 2014 "Concerning the welfare of rabbits in breeding units" (C-2014/24303). The Journal of the Belgian Government. 19.08.2014, 6061-6064. URL: http://www.vvsg.be/veiligheid/brandweer/brandweerhervorming/Documents/KB%202014.06.29%20personeelsplan.pdf (accessed 08/01/2017).
- ⁿ Austrian Consolidated Federal law 2004 Entire legal provision for the first animal welfare regulation. GBBI. II no. 485/2004. URL: https://www.ris.bka.gv.at/Geltende-Fassung.wxe?Abfrage=Bundesnormen&Gesetzesnummer=20003820 (accessed 08/01/2017).
- ¹ Animal welfare and livestock breeding regulations in the version of the notice of 22 August 2006 (Federal Law Gazette I, p.2043), most recently amended by Article 1 of the Ordinance of 14 April 2016 (Federal Law Gazette I, p. 758). URL: http://www.gesetze-im-internet.de/tierschnutztv/ (accessed 08/01/2017).
- ¹ PVE (2006) Productschappen Vee, Vlees en Eieren. Verordening Welzijnsnormen Konijnen. Zoetermeer, Nederland. (Product Boards for Livestock, Meat and Eggs. Rabbit Welfare Standards Regulation). URL: http://www.wrsa-deutschland.de/uploads/media/Kaninchenverordnung_NL_2008.pdf (accessed 08/01/2017).
- *Swiss Animal Protection Ordinance of 23 April 2008. URL: http://www.admin.ch/opc/de/classified-compilation/20080796/index.html (accessed 08/01/2017).

Concluding remarks

The usual process of domestication involves selection for docile traits, leading to a reduced fear of humans. This has not occurred in rabbits, and has important implications for their ability to cope with captive conditions. Welfare in commercial rabbit farms may be greatly improved by selective breeding to reduce aggression and fear of humans. Reducing fear and stress has the potential to reduce aggression in group-housing systems, which is currently a significant problem for farmed rabbits.

Rabbits are a social species and opportunities to perform social behaviours are critical for their welfare. However, current housing systems preclude the development of stable social hierarchies, which are necessary to manage aggression in social groups. Aggression can never be eliminated in rabbits, since it is how rabbit groups establish and maintain their hierarchy, but the high levels of aggression and injury in group-housed does in current systems are a significant source of pain and distress. A key priority is to develop and improve housing systems that promote stable hierarchies in breeding does and bucks.

Increasing space and environmental complexity by transitioning to park systems has high welfare potential,

though there are still some problems with injuries and aggression. Few of a rabbit's welfare requirements are fulfilled by cage systems, which are too small to allow normal locomotion or mother-young separation, and provide inadequate environmental complexity to promote rewarding behaviours. Cages do not allow group-housing of breeding rabbits, but fattening rabbits are increasingly group-housed in cage systems and small pens. In these systems, high stocking densities and limited space preclude conspecific avoidance and lead to increasing behavioural restriction as fattening rabbits grow. Successful group housing requires space and enrichment that cannot be provided in cage systems or pens stocked at high density.

A possible hurdle to overcome is the cost of higher welfare systems, as rabbit meat from barren cage systems is already more expensive than chicken or pork ¹³⁶. However, consumers are becoming increasingly interested in farm animal welfare ^{119,361,362} and are often willing to pay for higher welfare standards ^{361,363}; this can be exploited by marketing that emphasizes the enhanced product quality that accompanies higher welfare systems ³⁶².

Even though they are the second most frequently farmed species in the EU, welfare standards for rabbits are currently lagging behind those for other farmed species.

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