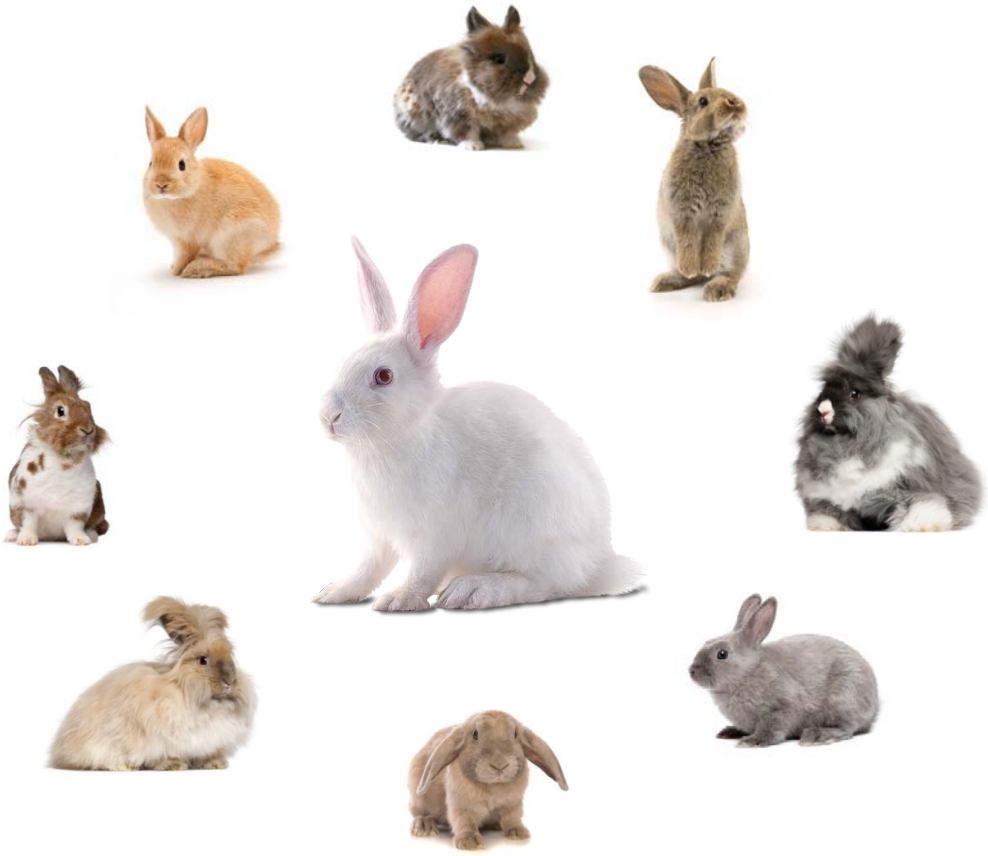
Domestic rabbit welfare



Welfare issues surrounding a multi-purpose animal

Master Thesis

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Abstract

The domestic rabbit (*Oryctolagus cuniculus*) is a multi-purpose animal. Kept in captivity to fulfill various roles (meat source, breeding stock, laboratory animal, pet, wool source and ornamental animal), this single species of animal encounters many different welfare problems related to its husbandry. Although some of these threats to rabbit welfare may be particular to a specific purpose, there are also stressors which are encountered by all captive rabbits. Scientific studies can provide knowledge on which to base recommendations for welfare improvement. However, most of these studies have so far been aimed at a single category of domestic rabbit. The present review aims to combine the knowledge gathered by welfare studies aimed at different categories of domestic rabbits. For each category, possible welfare problems are presented by comparing common husbandry practices to a definition of good rabbit welfare. Previous research of domestic rabbit welfare is discussed, with an emphasis on the welfare indicators used as a basis for their recommendations. It is concluded that together, welfare studies aimed at different categories of domestic rabbits have provided sufficient knowledge of the welfare effects of a rabbit's physical environment. Possible causes of poor welfare such as cage size, stocking density and enrichment have received extensive scientific attention. The topics of nutrition and handling by human caretakers have also been studied sufficiently to provide welfare recommendations. Therefore, it is suggested that future domestic rabbit welfare studies are aimed at possible welfare problems which have not yet received sufficient attention. For all categories of rabbits, providing a suitable social environment remains a challenge. The social demands of adult males in particular require further study. Also, welfare problems faced by Angora rabbits and ornamental rabbits require validation and suggestions for improvement.

Contents

1. Introduction

The domestic rabbit (*Oryctolagus cuniculus*) is successfully reared in captivity for different purposes, ranging from house pet to meat source[1]. Living in captive conditions provides these rabbits with certain benefits their wild counterparts do not have. For example, captive-reared rabbits no longer have to spend most of their time and energy looking for food and water, they can easily be provided with veterinary care in case of health problems and fear of predation is no longer an issue. However, life in captivity may also pose threats to the welfare of domestic rabbits. A captive environment has been a source of welfare problems for different species of animals, both wild and domestic[2]. This has been ascribed to the presence of stressors over which captive animals have no control and from which they cannot escape [3]. This seems a reasonable suggestion, as captive animals are forced to cope with artificial environments which often differ greatly from the circumstances in which their ancestors evolved. Whether an animal is likely to cope with life in captivity appears to depend greatly on the degree to which it can still act on its natural, species-specific motivations within its captive environment [2]. When adequate responses to such motivations are thwarted by captivity, animal welfare may be compromised.

The welfare challenges faced by an animal reared in captivity are often particular for the purpose that animal serves. For example, the care and management of farm animals will often be very different from that of companion animals. This results in different captive conditions and stressors with which an animal will have to cope. The domestic rabbit is an unusual species in that this single species is reared for many different purposes, with accompanying differences in husbandry [1]. So far, research efforts into the improvement of domestic rabbit welfare have for the most part been aimed at a specific category of rabbits, such as rabbits reared for their meat or those reared in laboratories. However, it has been suggested that knowledge of possible welfare improvement gained by studying animals used for one purpose could also be applied to the care of those belonging to a different category [4]. For example, although the experimental circumstances (such as cage sizes) used in welfare studies aimed at one category of rabbits may not be directly comparable to the circumstances experienced by all other categories of domestic rabbits, the resulting welfare recommendations (e.g. to provide larger cages) could be relevant to all domestic rabbits reared in captivity. Therefore, combining the knowledge gathered by welfare studies based on different categories of domestic rabbits would be useful.

There are several different categories of domestic rabbits which represent large numbers of animals in captivity that are unlikely to decline in the near future. Providing these categories with recommendations for welfare improvement could therefore impact the lives of many rabbits. The following categories of domestic rabbits will be discussed as part of this review:

- **Fattening rabbits.** Rabbits are an increasingly popular source of meat [5], with over 1.8 million tons of rabbit meat having been produced in 2012 [6]. Due to their size, nutritional requirements and reproductive potential, rabbits are considered a suitable (micro)livestock species under many different circumstances [e.g. suitable for production in lesser developed countries [1,7]].
- **Breeding rabbits.** Reproductive stock is necessary to produce the increasing numbers of domestic rabbits required not only for rabbit farms, but also for all other categories of

domestic rabbits. These breeding does and bucks are kept for the main purpose of producing offspring.

- **Laboratory rabbits.** The domestic rabbit is also a standard laboratory animal. In the lab, rabbits are used for numerous different purposes. For example, they are used to develop new surgical techniques or to test new drugs on [8]. Transgenic rabbits (carrying foreign genes within their original genome) are a special subgroup of laboratory rabbits. They are used as an animal model for a variety of human diseases [8,9]. Additionally, they are used for the production of pharmaceutical products (such as hormones, proteins and vaccines) in their blood and milk [8,10].
- **Pet rabbits.** Rabbits are increasing in popularity as a house pet across the world, due to their appearance, interactive nature and relatively low maintenance costs [1,11].
- **Angora rabbits.** Angora rabbits are kept as a source of Angora wool, a high-quality luxury fibre[1]. Angora fibre production is the third largest animal fibre industry in the world. It differs from other wool types in that Angora fibres have a very low density, creating a very light and soft wool[12].
- **Ornamental rabbits.** Different types of so-called ornamental breeds of domestic rabbit are kept for show or exhibition purposes [1]. These rabbits are selected and bred solely for their exterior features. Rabbit shows are being organized by rabbit breeder organizations all over Australia, Europe and North-America (e.g. American Rabbit Breeders Association, The Australian Show Rabbit Council, The British Rabbit Council).

By providing an overview of the welfare situations of these different categories of domestic rabbits, this review aims to produce future directions for rabbit welfare research. For each category of domestic rabbits, common husbandry practices and possible associated welfare problems will be described. Also, welfare studies based on these categories will be discussed, with a focus on the welfare indicators used and the suggestions for welfare improvement they have produced. Such an overview of domestic rabbit welfare will allow for the identification of welfare problems which are still lacking in scientific attention. Such shortcomings in knowledge of rabbit welfare could be due to an altogether lack of studies aimed at a specific welfare problem, or due to a lack of diversity in the types of welfare indicators which have been used. The overview of domestic rabbit welfare provided in this review could also prevent redundant research, as could happen when very similar welfare problems are studied separately for different categories of rabbits. In order to place all different welfare studies produced per category of domestic rabbits in a single framework, this review will start with a definition of good animal welfare in general and its application to domestic rabbits in particular.

2. Rabbit welfare

2.1 Animal welfare

The concept of animal welfare is complex. To this date, there is much debate about how it should be defined. At its basis, animal welfare describes an animal's state in its current environment [13]. This state can range between the two extremes of good/positive and bad/negative animal welfare [14,15]. An animal's current state within that continuum is determined by whether or not the animal can fulfill its own needs [14]. For example, a deficiency of energy or nutrients will lead to a need for food. The possible welfare problem of hunger can be averted when this need can be fulfilled by finding and eating suitable food. For an animal in captivity, a state of good welfare can be reached only when all of an animal's needs can be fulfilled within its captive environment [14,16]. This has been translated into a definition of animal welfare which suggests that an animal is in a good/positive welfare state when it has the freedom to adequately react to:

1. hunger, thirst or incorrect food;
2. thermal and physical discomfort;
3. injuries or diseases;
4. fear and chronic stress*, and thus,
5. the freedom to display normal behavior patterns that allow the animal to adapt to the demands of the prevailing environmental circumstances and enable it to reach a state that it perceives as positive [15].

This definition of good welfare [an adaptation of *the five freedoms* originally proposed by the Brambell Committee (1965)] does not only take into account the basic requirements for physical health of an animal (as described by freedom 1, 2 and 3)[17,18]. Rather, it also includes several more recent developments in the understanding of animal welfare. First of all, it acknowledges the existence and influence of an animal's affective state (freedom 4, 5)[14,16,19–21]. An animal could be considered as being in perfect physical health, yet still be experiencing poor welfare. For example, negative affective states such as fear and boredom due to lack of stimulation from their environment are recognized as threats to good welfare [14,20]. Secondly, both negative and positive affective states are appreciated as aspects of animal welfare (freedom 4, 5)[15,19]. Good animal welfare is not only the absence of negative affective states such as fear or frustration, but also the presence of positive affective states such as happiness and contentment [19,21]. The given definition of good animal welfare also takes into account an animal's ability to adapt to its environment (freedom 5). According to this definition, the presence of a negative affective state, such as fear, in itself will not necessarily lead to a decrease in animal welfare [15,19,22,23]. Only when an animal does not have the ability to adequately react to a fear-inducing stimulus (e.g. by performing avoidance behavior), will its welfare be compromised. Instead of a complete avoidance of stimuli which may provoke negative affective states, animals should be able to appropriately respond to such stimuli, thereby allowing them to perform a larger range of their natural behaviors [15,19]. This also implies that welfare should be considered over a certain period of time, not as a single static measurement [15]. In the previous

* Stress is defined as an animal's response to any threat to homeostasis (i.e. to a stressor)[23,24]. In this review, the term stress only describes a response which is thought to have a deleterious effect on an individual's welfare (sometimes described in other publications by the term 'distress'). Chronic stress occurs when an animal cannot adapt (physiologically or behaviorally) to the (repeated) presence of a stressor and a state of stress is maintained.

example, the presence of fear at one point in time does not immediately determine an animal's welfare status. Rather, whether it is able to adequately cope with that fear over time should be taken into account. Finally, the importance of an animal's behavioral repertoire is included in our definition of good animal welfare (freedom 5)[15]. The concept of ethological or behavioral needs implies that an animal's welfare is decreased when it is not capable of performing its normal pattern of behavior [18,25]. It is then assumed that an animal performs such behaviors because it is motivated to do so, either because the behavior will lead to direct physiological consequences (e.g. eating will decrease hunger) or because the performance of the behavior is rewarding in itself (e.g. positive social interactions, grooming behaviors)[19,25,26]. In order to achieve good welfare, an animal should therefore be able to act upon its motivations.

2.2 Domestic rabbit welfare

Good welfare according to the definition described above may look very differently depending on the species it is applied to. For example, what is considered a behavioral need for one species may be absent from the behavioral repertoire of another. Therefore, knowledge of the species under discussion is important when determining their welfare status. The domestic rabbit is descended from the European rabbit and asides from a physiological comparability, it has retained many behavioral similarities as well [27,28]. For all of the different categories of domestic rabbits discussed in this review, their welfare status is mostly determined by the captive environment that is created for them. Although these categories of rabbits may be presented with different environments and stressors which could compromise their welfare, there are also certain general requirements for good rabbit welfare. First, domestic rabbits are in a positive welfare state when they are free to adequately react to hunger, thirst and inadequate food. Therefore, rabbits should be able to find appropriate food and water within their captive environment. Domestic rabbits are obligate herbivores. Furthermore, their teeth and digestive physiology are specifically adapted to the ingestion of foods high in fibre. The digestive system of rabbits involves caecotrophy, where a specific type of faeces is re-ingested for its nutritional value [27,28]. This re-ingestion tends to take place during a quiet, undisturbed period [e.g. wild rabbits usually perform caecotrophy within their burrow [28]]. To ensure good welfare according to the first freedom, rabbits should be provided with a plant-based diet high in fibre content, as well as opportunities to perform caecotrophy. According to the second freedom, domestic rabbits should be free to adequately react to thermal and physical discomfort. As for thermal discomfort, rabbits are mostly sensitive to higher ambient temperatures as they are unable to sweat or pant to dissipate excess body heat [28,29]. A suitable ambient temperature is considered to lie within the range of 13 to 20 ^{o}C [30]. To ensure physical comfort, rabbits should have enough space to adopt comfortable resting postures and perform unrestricted forms of locomotion. Rabbits' feet lack footpads, making them vulnerable to abrasive surfaces [28]. To ensure good welfare, rabbits should be able to rest and move on a surface which does not cause discomfort to their feet. Also, rabbits are extensive groomers, keeping their fur and feet clean and dry [27]. Therefore, they are likely to experience discomfort from being housed in unhygienic conditions where they cannot keep clean. The third freedom states that domestic rabbits should be free to adequately react to injuries and diseases. Within their captive environment, rabbits should have the opportunity to avoid such health problems. For example, they should be able to avoid soiled areas within their enclosure in order to prevent excessive contact with pathogens. Also, in the case of sickness or physical injury, an adequate response to enable timely recovery would be to find a suitable resting place in the absence of further stressors. Fourth, domestic rabbits should be free

to adequately react to fear and chronic stress. All rabbits are prey animals, whose survival depends on the avoidance of predators. This is usually accomplished by sprinting to the protection of cover, formed by vegetation or underground burrows [27,28]. In the wild, rabbits regularly survey their surroundings for the presence of threats by raising either just their heads or their entire body onto their hind legs [28]. These behaviors indicate the possible presence of a predator could be an important stressor for domestic rabbits. This is relevant as all categories of domestic rabbits are forced to live in close contact with humans. Being in the presence of and even handled by humans is a likely source of fear for a prey animal, even when it is a domesticated species [31]. Decreasing rabbits' fear of human handlers or allowing for an adequate response (i.e. hiding when scared) are therefore necessary to ensure good welfare according to the fourth freedom. Finally, domestic rabbits should be free to display normal behavior patterns which enable them to adapt to their captive environment and reach a positive affective state. For domestic rabbits, social behaviors are very important. In the wild, rabbits usually live in groups with social hierarchies. Each group is formed by both adult males and females, and any present offspring [28]. Males and females form separate linear dominance hierarchies, which are established by fighting [32]. Within the group, the males defend the group's territory while the females dig burrows as nesting sites within the territory. Both older males and young males reaching puberty may be driven from a group and lead solitary lives [28]. Females spend their entire life in a group, usually the one they were born into. As for their maternal behavior, female rabbits provide very limited maternal care. Does prepare a nest for their offspring a couple of days before birth [33]. After birth, a doe will clean and nurse her kits and leave the nest. Until the kits wean at about 25 days of age, they are nursed once or twice a day for only a few minutes. The doe keeps her kits protected from the outside world by closing off the entrance to the nest every time she leaves it [28]. Another important behavior pattern for rabbits is foraging. In the wild, rabbits spend most of their active time grazing on grass and vegetation. This means that when domestic rabbits are able to consume all of their food within a short period of time (as is the case when they are fed exclusively on commercial pellets), they are faced with a large period of their active time to be filled with other activities. This could influence domestic rabbit welfare, as boredom is considered a negative affective state [20]. Furthermore, consistently frustrating a rabbit's ability to act upon its behavioral needs could lead to chronic stress, as the absence of suitable substrates for their normal behavior patterns (such as a social partner or gnawing material) could be considered stressors from which the rabbit cannot escape.

2.3 Measuring animal welfare

In order to objectively assess whether an animal is in a state of positive welfare in its current environment, measurable indicators of animal welfare are necessary. Many different types of indicators have been used in animal welfare studies. Most of these welfare indicators can be classified as either physiological or behavioral. Physiological parameters can be used as indicators of a variety of possible welfare problems. Firstly, there are measurable indicators which reflect the physical health of an animal. Examples are symptoms of disease, physical injuries, weight, body temperature and mortality [4]. These health indicators allow for the assessment of whether an animal is experiencing good welfare according to the first, second and third freedoms of the definition of animal welfare. Physiological parameters can also be used as indicators of stress, which can be a cause of poor welfare according to the fourth freedom. Commonly used examples of such parameters are heart rate, body temperature and products of HPA axis activity such as

glucocorticoids [23]. There are several suggested physiological indicators of positive affective states, such as oxytocin concentration and heart variability [4,19]. However, as of yet these have only rarely been used as part of animal welfare assessment. Physiological indicators are far more commonly used for the assessment of causes of negative welfare.

Similar to physiological indicators, behavioral parameters can be used as indicators of various different welfare problems [18]. Behavioral indicators of an animal's health status include food intake, alertness and the level of interest in its surroundings. The presence of injury, disease or discomfort could also be accompanied by specific pain-related behaviors, such as decreased or abnormal locomotion. Behavioral indicators of stress include changes in an animal's normal behavior pattern, such as the performance of abnormal behaviors [4]. It is important to note that stress with different underlying causes (e.g. social stress, boredom, inability to perform behavioral need) will result in the performance of different behavioral indicators of stress [34]. There are behavioral parameters indicative of stress in general, but also indicators of the effects of specific stressors. For example, social stress due to individual housing could lead to the performance of social grooming behaviors on unsuitable substrates, whereas elements of the environment which induce fear can be assessed by the performance of avoidance behavior [4]. Whether an animal is dealing with fear or stress can also be assessed by various behavioral tests which take place outside of its current environment. For example, the open field test is commonly used to assess emotional reactivity or anxiety, which influence an animal's ability to cope with stressors. During this test, an animal is placed in a novel, empty arena. Then, behavioral measures such as defecation and locomotion are measured and used as a reflection of the animal's stress level [34]. Behavioral indicators can also be used to assess whether an animal is capable of performing normal behavior patterns to reach a positive welfare state. A comparison of behaviors performed in captivity to those of wild conspecifics is often used to assess whether an animal's environment lives up to the fifth freedom of good welfare [35]. Examples of behavioral indicators of a positive affective state are the performance of play behaviors [36] or strongly preferred behaviors (i.e. which qualify as a behavioral need)[19]. Conversely, the absence of play behaviors or failing attempts at satisfying behavioral needs could indicate welfare is compromised. Finally, preference and motivation tests can be used to determine an animal's preferences and how much these are valued [18]. Their results can be used as an indicator of what an animal finds the most comfortable environment, the least fear- or stress-inducing environment or simply the environment which allows it to reach a more positive affective state.

In order to assess an animal's welfare status, it is recommended to use a combination of different welfare indicators [37]. This recommendation is based on the problems of interpretation which arise when using only a single indicator of welfare. Many of the responses that are measured as a welfare indicator could signify either a negative or positive affective state. An elevated heart rate, often used as a physiological indicator of stress, could also be caused by general activity or even a positive affective state such as excitement. The same applies to increased levels of HPA axis activity [23]. Behavioral indicators of animal welfare may also be difficult to interpret. An example is the open field test. An animal displaying a high level of locomotion during this test could be considered to be experiencing fear or stress, as its activity implies nervousness. However, the same animal could be labeled as stress-free, because it is relaxed enough in the novel environment to explore instead of freezing up with fear [34]. These examples show that using a single measure of stress could lead to wrong conclusions about an animal's welfare status. Using comparisons of wild behaviors to those performed in captivity may also be inadequate as the sole basis for welfare assessment [35]. For

example, behaviors performed in response to predators may not occur in captivity. This could simply be a reflection of an absence of threatening stimuli within the captive environment, instead of an inability to perform natural behavior patterns. By combining several different types of welfare indicators, a correct interpretation is much more likely. For example, when an animal's current environment does not allow for the performance of a certain behavior that is expected to be a behavioral need and this observation is accompanied by physiological indicators of stress, the case for poor welfare is much stronger.

2.4 Measuring rabbit welfare

Which welfare indicators are used to assess the welfare status of an animal may differ according to the species, or even the purpose, of the animal. Domestic rabbits have species-specific physiological and behavioral responses to be measured as indicators of welfare. Additionally, different categories of domestic rabbits will provide opportunities for the measurement of different welfare indicators. For example, pet rabbits are less likely to be available for the assessment of blood parameters than laboratory rabbits. Therefore, an overview and explanation of commonly used welfare indicators in domestic rabbit welfare is provided (Table 1). As for physiological parameters of health, mortality is most commonly used [37]. Health status can also be assessed using estimations of body condition and energy balance. The prevalence of diseases or injuries is often used to assess possible detrimental effects of domestic rabbits' captive environment. Finally, bone quality (often measured as bone strength) is a physiological measure of health which is only measurable post-mortem. Physiological indicators of stress are also commonly used to measure domestic rabbit welfare. Body temperature and heart rate have been measured, as well as glucocorticoid levels in blood, urine or faeces. In rabbits, both cortisol and corticosterone have been used as indicators of HPA axis activity [38]. Additional haematological parameters (such as neutrophil/lymphocyte ratio and concentrations of enzymes related to stress response) may also be used [39]. Fluctuating asymmetry is an indicator of stress which can only be measured post-mortem. It is a degree to which bilateral traits differ from perfect symmetry, indicating non-identical development on different sides of the body [40]. Fluctuating asymmetry reflects a domestic rabbit's ability to develop properly in its captive environment, with increasing values of asymmetry indicating a limited ability to develop. For fattening rabbits, respiratory distress has been measured as a sign of stress during gas stunning prior to slaughter [41].

As for behavioral welfare indicators, observations of a rabbit's behavioral repertoire in its captive environment is used most often. This allows for the assessment of changes in behavior due to (experimental) changes in environment. These observations also provide information about the performance of abnormal behaviors such as stereotypic behaviors, which are considered a behavioral sign of stress. For rabbits, most behaviors which are classified as abnormal are natural behaviors performed on unsuitable substrates. The performance of gnawing and pawing (digging) behaviors for example are very much a part of the wild rabbit's behavioral repertoire. However, when these behaviors are performed on unsuitable substrates (such as the bars of a cage or a cage floor), it can be used as an indicator that the current environment does not allow for the successful performance of natural behaviors [37]. Feed intake may be used as a behavioral indicator of health, but also to deduce preferences between different food sources. Tests of preference and motivation are also used to evaluate how domestic rabbits value other aspects of their environment, such as cage dimensions. Several behavioral tests have been used to determine whether domestic rabbits are experiencing fear and/or stress. These tests include approach and handling tests to determine

whether a rabbit will readily approach a human or how it behaves while being in close contact to one. Similarly, novel object tests measure a rabbit's fear towards an unfamiliar item in its environment, which can also be used as a measure of emotional reactivity and anxiety. The aforementioned open field test is often used for the same purpose. The emergence test measures general fear levels. A rabbit is placed inside a closed start box and its attempts to emerge from it are measured after it has been opened [42]. Also, tonic immobility tests are common in rabbit welfare studies. During such a test, fear towards humans is measured by picking a rabbit up and placing it on its back. This may or may not induce a state of immobility. Number of attempts necessary to induce this state is then used as a measure of fear, with higher numbers of attempts required indicative of a lower fear level. Finally, the behavior of domestic rabbits has been used to assess whether or not they are experiencing pain. Parameters of pain include walking speed, posture and facial expression [43,44].

Table 1 Overview of welfare indicators used in domestic rabbit welfare studies.

Welfare indicator	**Description**	**Example study**
Physiological indicators		
Health		
Body condition[2,3]	Estimation of muscle and fat mass in relation to the rabbit's size and weight.	Rosell & de la Fuente, 2008
Bone quality[1]	Resistance of bones to fracture, measured after dissection.	Buijs *et al.*, 2012
Disease/Injury prevalence[1,2,4,6]	Number of rabbits presenting symptoms of disease or injury.	de Jong *et al.*, 2008
Energy balance[2]	Comparison of empty body composition at different stages (estimated after slaughter).	Xiccato *et al.*, 2004a
Mortality[1,2, 6]	Number of deaths occurring over a certain (experimental) period.	Bennegadi *et al.*, 2001
Stress		
Body temperature[2]	Changes in a rabbit's body temperature are measured as a response to stressors.	Graf *et al.*, 2011
Fluctuating asymmetry[1]	Index of symmetry of bilateral traits, reflecting a rabbit's ability of normal (symmetrical) development.	Tuyttens *et al.*, 2005
Glucocorticoids[1,2,3]	Levels of glucocorticoids (such as corticosterone and cortisol) are measured in rabbits' blood or faeces.	Buijs *et al.*, 2011a
Haematological parameters[1]	Measurement of blood constituents related to stress other than glucocorticoids (e.g. concentration of glucose and enzymes such as creatine kinase, neutrophil/lymphocyte ratio).	Yakubu *et al.*, 2008
Heart rate[3]	Changes in a rabbit's heart rate are measured as a response to stressors.	Canali *et al.*, 2000
Respiratory distress[1]	Gasps and other indications of difficulty to breathe are measured.	Llonch *et al.*, 2012
Behavioral indicators		
General behavioral observations[1,2,3,4]	The behavior of rabbits is recorded within their regular and/or modified environment. Different types of behaviors (e.g. aggression, grooming, locomotion, posture, stereotypic behavior, use of available space) can be scored.	Ribikauskas *et al.*, 2010

Feed intake[1,2]	Comparison of voluntary use of food sources (e.g. pellets, food items used as enrichment).	Princz *et al.*, 2007
Preference test[1,2,3,4]	Rabbits are given the choice between different situations (e.g. different floor types, cage sizes, etc.). Preference is usually measured as time spent on/in/near the preferred option.	Matics *et al.*, 2003
Motivation test[4]	A degree of preference is measured by making rabbits work for access to different situations (e.g. a larger cage, the presence of conspecifics). It is then assumed that the option that is worked for the most is the most preferred.	Seaman *et al.*, 2008
Pain		
Facial expression[3]	Different aspects of a rabbit´s facial expression are measured as an indication of the degree of pain it is experiencing. These are tightening of eyelids, position of whiskers, nose shape and ear position.	Keating *et al.*, 2012
Stress		
Approach test [1,2,3]	Latency to approach the experimenter and number of approaches are recorded as measures of timidity.	Csatádi *et al.*, 2005
Emergence test[1]	A rabbit is placed inside a closed start box. After opening it, its attempts to leave the box and enter an arena are recorded.	Zucca *et al.*, 2012a
Handling test [1,4]	A rabbit´s behavior is recorded while being handled (i.e. picked up by or placed on lap of experimenter).	Jezierski & Konecka, 1996
Novel object test [1,3]	Behavior of rabbits is recorded while in the presence of an unfamiliar object. Behaviors such as fleeing from or approaching the novel object are recorded.	Pongrácz & Altbäcker, 1999
Open field test[1,3,4]	A rabbit is placed inside a barren enclosure, i.e. there are no possible hiding places. Its behavior is then recorded (e.g. escape attempts, moving towards centre of enclosure). Often, the floor area of the enclosure is divided into squares and line-crossings are recorded as a measure of exploration.	D´Agata *et al.*, 2009
Tonic immobility test[1,3]	The experimenter attempts to induce immobility by placing a rabbit on its back. Number of attempts required to induce immobility and duration of immobility are recorded.	Trocino *et al.*, 2013

Welfare indicator Name of the indicator described and categories of domestic rabbits indicator has been used on, with [1] = fattening rabbits, [2] = breeding rabbits, [3] = laboratory rabbits, [4] = pet rabbits, [5] = Angora rabbits and [6] = ornamental rabbits. *Description* How indicator is used to measure rabbit welfare. *Example study* Researchers performing an experiment in which indicator was used.

3. Rabbit welfare studies

The welfare studies discussed in this review were found using the search engines Google Scholar, PubMed and Web of Science. These were prompted to search for the keywords 'rabbit welfare' and 'rabbit [specific welfare problem]' (e.g. 'rabbit stocking density', 'rabbit enrichment', etc.). Additionally, any rabbit welfare studies used as references in found publications were added. Review articles were only used when they provided information about the welfare indicators used in their references. As mentioned, studies of domestic rabbit welfare have often been aimed at only a single category of domestic rabbits. This has resulted in an uneven distribution of welfare studies over the different categories (Fig. 1). Studies that were aimed at multiple categories of domestic rabbits have been included in the discussion of all of these related categories. The welfare of fattening rabbits has received by far the most scientific attention with over 80 studies. Pet rabbits, Angora rabbits and ornamental rabbits have been studied the least, with under 10 studies for each of these categories.

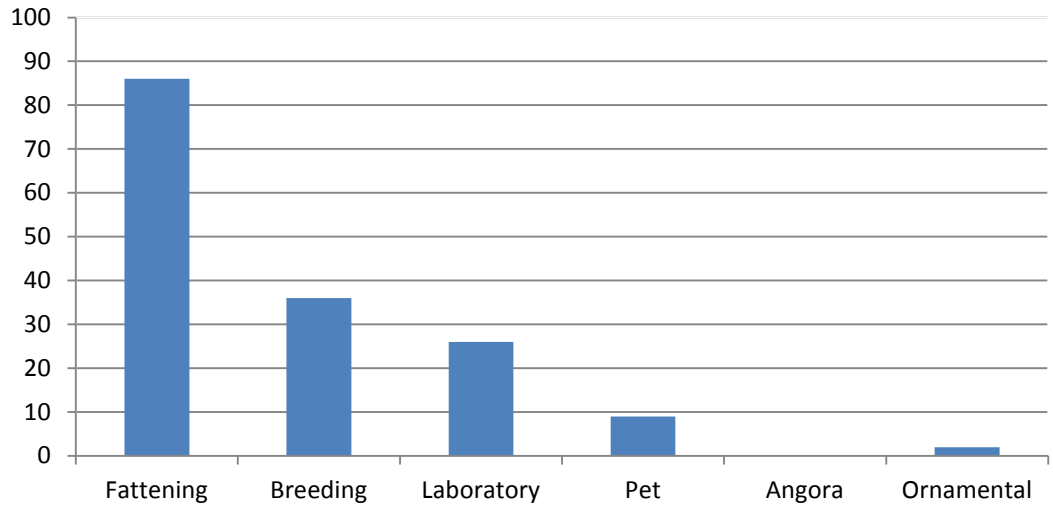

Figure 1 Number of welfare studies discussed in this review per category of domestic rabbits.

3.1 Fattening rabbits

Several practices are common to all rabbits which are farmed for their meat (hereafter called fattening rabbits). Kits are born inside a nest box, in which a nest has been prepared by the doe from her own fur and any additional nesting material provided to her (Figure 2A). During the first three weeks of their life, the kits are nursed once a day and only feed on the doe's milk. After these three weeks, the kits start exploring outside of their nest box, which gives them access to the doe's food and water. They will continue to nurse until they are weaned at an age of 28-35 days. At weaning, fattening rabbits are either moved to a new cage or the doe is removed while the fatteners remain in the same cage [45]. Their cages are typically made of metal wire and are barren except for the presence of feeders and drinkers [46](Figure 2B). Fattening rabbits are usually fed exclusively on pellets. It is common practice to house them in groups for the duration of their lives [7,45]. However, the composition of these groups will likely change on several occasions: after weaning, prior to transport to the abattoir and during lairage prior to slaughter. When fattening rabbits have reached slaughtering age [at about 73 days of age [45]], they are caught and housed in crates which are stacked on multi-level roller stands [47](Figure 2C). These are usually transported to the abattoir by truck [45]. At the abattoir, the rabbits are either moved to a cage for lairage or slaughtered directly. Stunning prior to slaughter is commonly performed by means of electrocution [41,48,49]. During the time between catching for transport and slaughter, fattening rabbits do not have access to food or water [47].

Figure 2 Common aspects of fattening rabbit husbandry, with young rabbits housed together with breeding doe (A), post-weaning rabbits housed as groups (B) and crates used for transport to abatoir (C).

3.1.1Welfare problems

The following practices of rabbit farming form potential threats to the welfare of fattening rabbits:

- **Health problems.** The health of fattening rabbits could be compromised due to regular farming practices. Although weaning practices are unlikely to be a threat to welfare due to their similarity to wild rabbits [28], the sudden change in diet could be a cause for health problems. Additionally, fattening rabbits spend their entire life indoors, housed in cages. This means air quality and hygiene levels could have a negative influence on rabbit health and comfort.

- **Housing conditions**, including:
    - **Stocking density.** Cage housing fattening rabbits could compromise welfare by limiting comfortable moving and resting space for the rabbits. It is possible certain natural forms of posture and locomotion cannot be performed when stocking densities are relatively high, as this decreases the available space per rabbit. Additionally, a lack of available space per rabbit could lead to (social) stress, as there may not be enough room to avoid aggressive group members.
    - **Group size.** Although group housing of fattening rabbits is in concordance with their natural social existence [28], it also produces several possible threats to their welfare. First of all, group housing and the establishment of a dominance hierarchy could lead to competition over access to feeders and drinkers inside the cage. Also, the establishment of a dominance hierarchy could lead to aggressive behaviors. These could lead to both social stress and injuries. When fattening rabbits do not have the opportunity to adequately respond to these social pressures, their welfare may be compromised. The risk of continued social stress could be increased for larger group sizes, in which it could be more difficult to establish and maintain a clear dominance hierarchy. The welfare threat posed by aggression amongst fattening rabbits may also increase with age, as available space decreases and rabbits become sexually mature. This could lead to housing conditions which are in contrast with natural conditions, where male rabbits leave their natal group after reaching puberty [28]. Finally, a larger group size could enable the spread of diseases, thereby threatening the health of fattening rabbits.
    - **Cage height.** The standard dimensions of cages used to house fattening rabbits do not allow them to stand upright on their hind legs. In the wild, this posture is a common occurrence [28]. Therefore, it is possible that the cage height used in commercial farms prevents fattening rabbits from displaying a natural behavior pattern, which could prevent them from reaching a more positive welfare state.
    - **Floor type.** The metal wire floors used to house fattening rabbits could be a source of discomfort. As rabbits lack foot pads, they could be very vulnerable to such discomfort and resulting injuries from bearing all their weight on metal wiring. On the other hand, wire floors do not allow manure and urine to build up inside the cage. This could lead to a more hygienic environment for the fattening rabbits to live in, consequently increasing their comfort levels. A cleaner cage could also be beneficial for the rabbits' health, as it decreases the probability of pathogens being present in the rabbit's direct environment.
    - **Enrichment.** In barren cages, fattening rabbits could be restricted in their behavioral repertoire. The inability to interact with their environment could lead to frustration, boredom and chronic stress. Asides from being a direct source of negative affective states, lack of enrichment could also prevent fattening rabbits from reaching a positive affective state through the performance of rewarding behaviors.
- **Handling.** Fattening rabbits are forced to interact with humans throughout their lives. As rabbits are prey animals, this contact could be a source of fear and stress.
- **Transport procedures.** Several aspects of transport procedures could be considered sources of fear and stress for fattening rabbits [50,51]. Being removed from their familiar environment, mixing with unfamiliar rabbits, being exposed to changes in temperature and noise and

being handled by personnel are all possible stressors. Also feed and water withdrawal could be a source of decreased welfare, as it limits the rabbits' response to hunger and thirst.

- **Slaughter procedures.** Finally, slaughter itself could be a source of stress and/or pain when performed inappropriately. Stunning procedures before slaughter have to be effective in order to prevent unnecessary pain. Furthermore, lairage prior to slaughter could also impact the welfare of fattening rabbits, due to possibilities of mixing stress and fear of a novel environment.

3.1.2 Welfare studies

The following possible welfare problems for fattening rabbits have received scientific attention (see Table 2 for overview):

Health problems. Digestive disorders amongst fattening rabbits appear to be a common welfare problem. They are the main pathological problem encountered on rabbit farms and are most common in weaned fattening rabbits [46,52]. Recently, the use of food restriction has been reviewed as a means of improving the health of post-weaning fattening rabbits [53]. It was found that restricting the food intake of rabbits changes their feeding behavior. When fed *ad libitum*, rabbits take in numerous small meals throughout the day. When food restriction is applied, rabbits consume all their feed within the next 8-16 hours, meaning they are potentially hungry for the remaining 8-16 hours a day. This would decrease their welfare according to the first freedom. However, rabbits on restricted feed have improved digestive health, improving their welfare according to the third freedom. This improvement in welfare has been measured as decreased mortality from digestive disease [53]. Additionally, it has been suggested that due to caecotrophy, rabbits are better able to respond to their hunger even in the absence of food [54]. Another possible welfare improvement could be reached by changing the fattening rabbits' diet. The amount of fiber in the rabbits' diet is believed to be a major influence on their digestive functioning, with fiber deficiency in particular being a cause of digestive disease and related mortality [55–60]. Therefore, providing fattening rabbits with a sufficient amount of fiber in their post-weaning diet is likely to improve their welfare. Additionally, maintaining a hygienic environment for the rabbits has been associated with a decrease in digestive disease occurrence, pathogen concentrations and mortality [56,61,62]. Possible detrimental health effects of a farm's air quality have received limited scientific attention. It has been suggested that fungal spores and bacteria are abundant in the air inside rabbit farms [63]. However, whether infective pathogens are present and in what concentrations has not yet been studied. Several studies measured air quality parameters (such as gas concentrations of ammonia) and reported that these were all within the acceptable range in terms of rabbit welfare [64,65].

In sum, health problems related to weaning practices appear to be a threat to rabbit welfare as digestive disorders are common causes of mortality. Adjusting the diet of fatteners appears to be the most suitable solution when only taking their welfare into account. Providing appropriate sources of fiber will decrease mortality without providing additional welfare problems such as limiting an adequate response to hunger. Regular cleaning and disinfecting of the rabbits' cages is recommended to reduce the possible spread of pathogens. As for air quality, the few studies that have investigated it as a possible welfare problem have concluded that gas concentrations in rabbit farms do not pose a threat to rabbit welfare.

Table 2 Overview of studies on fattening rabbit welfare.

Welfare problem(s)	Welfare indicator(s)	N	Age (days)	Study duration (days)	Sex	Author(s)
Health problems						
General health status - effect of hygiene level	Mortality	672	25/35	31/21	-	Garrido *et al.*, 2009
General health status - surveillance on farms	Disease occurrence	-	-	-	f/m	Rosell, 2003
General health status - surveillance on farms	Disease occurrence	-	-	-	f/m	Rosell *et al.*, 2009
Digestive disorders - effect of nutrition	Disease occurrence, mortality	-	-	-	-	de Blas, 2013
Digestive disorders - effect of nutrition and sanitary status	Disease occurrence, mortality	-	-	-	-	de Blas *et al.*, 2012[1]
Digestive disorders - effect of fibre content provided in diet	Disease occurrence, mortality	-	-	-	-	Gidenne, 2003[1]
Digestive disorders - effect of feed intake limitation	Behavioral observation, mortality	-	-	-	-	Gidenne *et al.*, 2012[1]
Digestive disorders - effect of fibre content provided in diet	Disease occurrence, mortality	2576	28-37	35-42	-	Gidenne *et al.*, 2013
Digestive disorders - effect of fibre content provided in diet	Mortality	1592	35	31	-	Grueso *et al.*, 2013
Digestive disorders - effect of fibre content provided in diet	Disease occurrence, mortality	-	-	-	-	Trocino *et al.*, 2013[1]
Housing conditions						
Stocking density - change of cage size and group size	Mortality, open field test, tonic immobility test	76	57	46	f/m	D'Agata *et al.*, 2009
Stocking density - change of change of cage size and group size	Mortality	502	28	42	f/m	Hamilton & Lukefahr, 1993
Stocking density, **floor type** - change of cage size and group size; larger enclosures received straw bedding	Mortality	184	35	48	f/m	Lambertini *et al.*, 2001 - experiment 1
Stocking density, **group size**, **floor type** - change of cage size and group size; change of cage size to maintain stocking density; larger enclosures received straw or wood shavings as bedding	Mortality	232	42	41	f/m	Lambertini *et al.*, 2001 - experiment 2
Stocking density, **floor type** – change of cage size; larger enclosures received straw bedding	Behavioral observation	50	35	42	f/m	Lehmann, 1987
Stocking density - change of cage size and group size	Preference test	-	28	17	f/m	Matics *et al.*, 2004
Stocking density - change of group size	Mortality	72	56	56	f/m	Mbanya *et al.*, 2004
Stocking density – change of cage size and group size	Behavioral observation	16	30	60	-	Metz, 1987
Stocking density - change of group size	Behavioral observation	90	30	40	f/m	Morisse & Maurice, 1997

Stocking density - change of cage size	Mortality	60	51	52	m	Paci *et al.*, 2013
Stocking density - change of cage size and group size: cage versus pen with straw litter versus open air enclosure on grass	Mortality, open field test, plasma glucocorticoid level	120	35	49	f/m	Pinheiro *et al.*, 2012
Stocking density, **floor type** - change of cage size and group size; larger enclosures received straw bedding	Behavioral observation	69	55	30	-	Ribikauskas *et al.*, 2010
Stocking density, **group size** - change of cage size and group size; stocking density maintained by changing only cage size	Injury occurrence (aggression)	230	35	42	f/m	Szendrő *et al.*, 2009
Stocking density, **floor type** - change of cage size; metal wire or metal slatted flooring	Behavioral observation, bone quality, open field test, tonic immobility test	320	29	42	f/m	Trocino *et al.*, 2004
Stocking density, **floor type** - change of cage size; metal wire, metal slatted, plastic slatted or straw bedded flooring	Bone quality, open field test, tonic immobility test	240	36	42	f/m	Trocino *et al.*, 2008
Stocking density, **group size** - change of group size and cage size; stocking density maintained by changing cage size	Behavioral observation, faecal and hair glucocorticoid level, open field test, tonic immobility test	456	35	41	f/m	Trocino *et al.*, 2014
Stocking density, **enrichment** - change of group size; presence of platforms and gnawing stick (provided simultaneously)	Fluctuating asymmetry, mortality	306	28	44	f/m	Tuyttens *et al.*, 2005
Stocking density, **enrichment** - change of group size; presence of gnawing stick	Behavioral observation	72	35-75	40	-	Verga *et al.*, 2004
Stocking density - change of group size and cage size	Bone quality	456	35	41	f/m	Xiccato *et al.*, 2013
Stocking density - change of group size	Body condition, haematological parameters, injury occurrence (aggression and floor type)	42	-	42	f/m	Yakubu *et al.*, 2008
Group size, **enrichment** - stocking density maintained by changing cage size, larger enclosures were enriched with platform	Bone quality	428	31-71	40	f/m	Combes *et al.*, 2010
Group size, **floor type**, **enrichment** - stocking density maintained by changing cage size; metal wire or plastic net flooring; presence of gnawing stick	Bone quality	176	-	-	f/m	Dalle Zotte *et al.*, 2009a
Group size - stocking density maintained by changing cage size	Behavioral observation, open field test, tonic immobility test	384	27	48	f/m	Filiou *et al.*, 2012
Group size - stocking density maintained by changing cage size	Behavioral observation, bone quality, injury occurrence (aggression)	360	32	31	f/m	Martrenchar *et al.*, 2001
Group size - stocking density maintained by changing cage size	Mortality	88	56	47	m	Paci *et al.*, 2013
Group size - stocking density maintained by changing cage size	Behavioral observation, bone quality, disease	378	31	41	f/m	Postollec *et al.*, 2006

	occurrence, injury occurrence (aggression), mortality					
Group size, **enrichment** - stocking density maintained by changing cage size; larger enclosures contained metal wire platform	Behavioral observation, disease occurrence, injury occurrence (aggression), mortality	428	31	41	f/m	Postollec *et al.*, 2008
Group size, **floor type**, **enrichment** - stocking density maintained by changing cage size; metal wire or plastic net flooring; presence of gnawing stick	Behavioral observation, injury occurrence (aggression)	176	35	42	-	Princz *et al.*, 2008a - experiment 2
Group size, **floor type**, **enrichment** - stocking density maintained by changing cage size; metal wire or plastic net flooring; presence of gnawing stick	Injury occurrence (aggression), mortality	176	35	42	-	Princz *et al.*, 2009
Group size - stocking density maintained by changing cage size	Behavioral observation, bone quality, injury occurrence (aggression), mortality	348	30	43	f/m	Rommers & Meijerhof, 1998
Group size - stocking density maintained by changing cage size	Behavioral observation, open field test, tonic immobility test	384	27	48	f/m	Trocino *et al.*, 2013
Sex composition group - all female, all male or mixed-sex group	Behavioral observation, injury occurrence (aggression), mortality	168	35	42	f/m	Szendrő *et al.*, 2012a
Cage height - presence of ceiling and different ceiling heights	Preference test	112	35	28	-	Princz *et al.*, 2008b - experiment 1
Cage height- presence of ceiling and different ceiling heights	Injury occurrence (aggression), mortality	156	35	42	-	Princz *et al.*, 2008b - experiment 2
Floor type, **stocking density** - metal wire or straw bedded flooring; change of cage size and group size	Behavioral observation, mortality	300	35	50	m	Dal Bosco *et al.*, 2002
Floor type - metal wire, plastic slatted or straw bedded flooring	Preference test	129	35	42	-	Gerencsér *et al.*, 2012
Floor type - metal wire, plastic slatted or straw bedded flooring	Preference test	129	35	77	-	Gerencsér *et al.*, 2014 - experiment 1
Floor type - metal wire, plastic slatted or straw bedded flooring	Mortality	126	35	84	-	Gerencsér *et al.*, 2014 - experiment 2
Floor type, **stocking density** - metal wire or partly straw bedded flooring; change of group size	Behavioral observation	124	35	42	f/m	Jekkel & Milisits, 2009
Floor type, **stocking density** - metal wire or straw bedded flooring; change of group size	Behavioral observation	120	35	42	f/m	Jekkel *et al.*, 2007
Floor type, **stocking density** - metal wire or straw bedded flooring; change of group size	Behavioral observation	240	35	42	f/m	Jekkel *et al.*, 2008
Floor type, **group size** - metal wire or straw bedded flooring; stocking density maintained by changing cage size	Behavioral observation	312	35	42	-	Jekkel *et al.*, 2010
Floor type - metal wire, plastic mesh, plastic slatted or wood board flooring	Preference test	-	21	49	-	Matics *et al.*, 2003
Floor type - metal wire or partly straw bedded flooring	Behavioral observation, disease occurrence, mortality, open field	384	32	40	f/m	Morisse *et al.*, 1999

	test, preference test					
Floor type - half metal wire, half straw bedded flooring	Preference test	-	35	-	-	Orova *et al.*, 2004
Floor type - metal wire or plastic slatted flooring with differing distances between slats	Behavioral observation	170	7	28	f/m	Petersen *et al.*, 2000
Floor type, **enrichment** - metal wire or plastic net flooring; presence of gnawing stick	Preference test	112	35	42	-	Princz *et al.*, 2008a - experiment 1
Floor type - metal wire or partly straw bedded flooring	Behavioral observation, preference test	48	35	35	-	Siloto *et al.*, 2008
Floor type, **enrichment** - platform made of metal wire or straw bedded plank ; platform with or without manure tray	Behavioral observation - space use within enclosure	168	35	42	-	Szendrő *et al.*, 2012b
Enrichment - presence of gnawing blocks	Block consumption, mortality	420	36	28	-	Bignon *et al.*, 2012a
Enrichment, **stocking density**, **transport** - presence of wooden platform; change of cage size; crated and transported	Behavioral observation, faecal glucocorticoid metabolites	672	30	45	f/m	Buijs *et al.*, 2011a
Enrichment, **stocking density** - presence of wooden platform; change of cage size	Behavioral observation	672	30	38	f/m	Buijs *et al.*, 2011b
Enrichment, **stocking density** - presence of wooden platform; change of cage size	Bone quality, fluctuating asymmetry, mortality	672	30	46	f/m	Buijs *et al.*, 2012
Enrichment - presence of birch twigs or onion bulbs	Disease occurrence, injury occurrence (aggression), mortality	90	35	55	f/m	Gugolek *et al.*, 2008
Enrichment - presence of gnawing stick made from different types of wood	Behavioral observation, feed intake	48	38	63	m	Jordan *et al.*, 2004
Enrichment - presence of gnawing stick	Feed intake, mortality	48	44	45/59	f/m	Jordan *et al.*, 2008
Enrichment - presence of slatted plastic platform	Behavioral observation, injury occurrence (aggression)	511	35	56	f/m	Lang & Hoy, 2011
Enrichment - presence of gnawing stick	Behavioral observation, injury occurrence (aggression), mortality	96	55	35	-	Luzi *et al*., 2003
Enrichment - presence of gnawing stick	Behavioral observation, injury occurrence (aggression), mortality	96	55	30	-	Luzi *et al.*, 2005
Enrichment, **group size** - presence of gnawing stick in larger groups; stocking density maintained by changing cage size	Gnawing stick consumption, mortality	336	29	42	f/m	Maertens & van Herck, 2000
Enrichment, **stocking density** - presence of plastic platform, hiding box and gnawing stick; change of group size	Injury occurrence (aggression), mortality	306	29	43	f/m	Maertens *et al.*, 2004
Enrichment - presence of gnawing blocks made of different materials	Gnawing block consumption, mortality	-	35	35	f/m	Maertens *et al.*, 2013
Enrichment, **floor type** - presence of platform; platform made of metal wire or plastic mesh	Behavioral observation - space use within enclosure	-	18	13	f/m	Mikó *et al.*, 2012a
Enrichment - presence of gnawing stick or roughaghe in metal wire trough	Mortality	264	36	35	-	Mirabito *et al.*, 2000

Enrichment - presence of 3 gnawing sticks made of different wood types	Preference test	180	35	42	-	Princz *et al.*, 2007 - experiment 1
Enrichment - presence of 3 gnawing sticks made of different wood types which were preferred during previous experiment	Preference test	150	35	42	-	Princz *et al.*, 2007 - experiment 2
Enrichment - presence of gnawing stick made from different types of wood	Behavioral observation, gnawing stick consumption	48	38	56	m	Princz *et al.*, 2007 - experiment 3
Enrichment - presence of gnawing stick made from different types of wood	Behavioral observation	72	35	40	-	Princz *et al.*, 2007 - experiment 4
Enrichment - presence of gnawing stick made from different types of wood	Gnawing stick consumption, injury occurrence (aggression)	156	35	42	f/m	Princz *et al.*, 2008c
Enrichment, **group size** - presence of gnawing stick; stocking density maintained by changing cage size	Behavioral observation, emergence test, mortality, tonic immobility test	108	40	39	f/m	Zucca *et al.*, 2008
Enrichment, **group size** - presence of gnawing stick; stocking density maintained by changing cage size	Behavioral observation, emergence test, tonic immobility test	108	40	39	f/m	Zucca *et al.*, 2012a
Handling						
Handling - daily handling directly after nursing until weaning	Approach test	30	0	28	f/m	Bilkó & Altbäcker, 2000 - experiment 1
Handling - timing of daily contact until weaning	Approach test	52	0	28	f/m	Bilkó & Altbäcker, 2000 - experiment 2
Handling - intensity and timing of contact during first week of life	Approach test	57[2]	0	28	f/m	Csatádi *et al.*, 2005
Handling - daily handling during first 20 days of life	Open field test	28	0	31-34	f/m	Denenberg *et al.*, 1977
Handling - intensity and timing of contact during first week of life	Approach test	61	0	28	f/m	Dúcs *et al.*, 2009
Handling - daily handling for 30 weeks	Handling test, mortality	112	10	200	-	Jezierski & Konecka, 1996
Handling - no handling or twice daily handling during first or second 10 days of life	Open field test	118	0	98	f/m	Kersten *et al.*, 1989
Handling - timing of contact during first week of life	Approach test	15[2]	0	28	f/m	Pongrácz & Altbäcker, 1999 - experiment 1
Handling - timing of contact during first week of life	Approach test, open field test	18[2]	0	28	f/m	Pongrácz & Altbäcker, 1999 - experiment 2
Handling - durability of reduced fear towards humans displayed by rabbits from previous experiments	Approach test, open field test, novel object test	28	0	8[3]	-	Pongrácz & Altbäcker, 1999 - experiment 3
Handling - daily contact during first week of life	Emergence test, tonic immobility test	34[2]	0	33	f/m	Zucca *et al.*, 2012b
Transport procedures						
Crating/loading, transport – smooth/gentle versus rough crating and loading methods; transport of 100 minutes	Haematological parameters, plasma glucocorticoid levels	384	82	-	m	Mazzone *et al.*, 2010

Crating/loading, transport – smooth/gentle versus rough crating and loading methods; position on multi-floor cages	Haematological parameters, plasma glucocorticoid levels	40	82	-	m	Vignola *et al.*, 2008
Transport, **slaughter** – crated and transported for 6 hours; slaughter after stunning (slaughter method not mentioned)	Body temperature, haematological parameters, heart rate, plasma glucocorticoid levels	400	85	5	f/m	Canali *et al.*, 2000
Transport – response to heat, cold, noise and mixing stress	Haematological parameters, plasma glucocorticoid levels	120	55	10	f/m	de la Fuente *et al.*, 2007
Transport – crated and transported for 100 minutes	Haematological parameters, plasma glucocorticoid levels	80	82	-	m	Giammarco *et al.*, 2012
Transport –duration, position on multi-floor cages	Haematological parameters, plasma glucocorticoid levels	156	60	-	-	Liste *et al.*, 2008
Transport – transport duration	Haematological parameters	80	-	-	m	Nakyinsige *et al.*, 2013
Slaughter procedures						
Lairage – duration and position on multi-floor cage	Haematological parameters, injury occurrence (bruising), plasma glucocorticoid levels	144	60	-	-	Liste *et al.*, 2009
Lairage, **transport** – duration	Injury occurrence (bruising), mortality	831[4]	63	21	f/m	Petracci *et al.*, 2008
Lairage, **transport** – duration	Injury occurrence (bruising), mortality	975[4]	63	21	f/m	Petracci *et al.*, 2010
Lairage – duration, mixing stress	Haematological parameters	18	90	-	m	Sabuncuoglu *et al.*, 2011
Stunning – electrical stunning with different voltages	Behavioral and physiological signs of recovery	30	-	-	f/m	Anil *et al.*, 1998 – experiment 1
Stunning – electrical stunning with different voltages and durations	Behavioral and physiological signs of recovery	40	-	-	f/m	Anil *et al.*, 1998 – experiment 2
Stunning – electrical stunning	Brain function	8	-	-	-	Anil *et al.*, 2000
Stunning - electrical stunning and cervical dislocation	Body temperature, haematological parameters	40	70	-	f/m	Guerrero *et al.*, 2007
Stunning – gas stunning, different gas mixtures	Behavioral signs of loss of consciousness, defaecation, open field test, respiratory distress	60	-	-	-	Llonch *et al.*, 2012
Stunning – electrical stunning with different voltages and frequencies	Behavioral and physiological signs of recovery	148	-	-	f/m	María *et al.*, 2001
Stunning, **slaughter** – gas stunning; slaughter without stunning	Haematological parameters	80	-	-	m	Nakyinsige *et al.*, 2014
Stunning, **slaughter** – electrical stunning; sticking	Behavioral observation, physiological signs of consciousness	1020	90	-	f/m	Rota Nodari *et al.*, 2008

Stunning, **slaughter** – electrical stunning; sticking	Behavioral observation, physiological signs of consciousness	1020	90	-	f/m	Rota Nodari *et al.*, 2009

Welfare problem(s) Possible rabbit welfare problem(s) examined in study with short description of experimental manipulations. *Welfare indicator(s)* List of indicator(s) used to measure rabbit welfare. *N* Number of study subjects used for experiment. *Age* Age of study subjects at start of experiment. *Study duration* Duration of experimental treatment. *Sex*: *f* female/doe, *m* male/buck. *Author(s)* Researcher(s) responsible for experiment. [1] = review article, [2] = N in number of litters tested, [3] = study duration in months, [4] = N in number of batches shipped to abattoir

Stocking density. Many welfare studies have focused on the effects of decreasing the stocking density of fattening rabbits. A decrease in stocking density can be accomplished in several ways: increasing cage size, decreasing group size or a combination of both adjustments (see Table 3 for range of cage and group sizes tested). Stocking densities ranging from 0.25 to 33 fattening rabbits per m^2 have been studied (Table 3). Decreasing the stocking density of group housed rabbits appears to positively influence the health of fattening rabbits. Although an influence on mortality was not always found [66–68], when there was a difference, it was in favor of a lower stocking density [69,70]. Additionally, a lower stocking density has resulted in a higher bone quality and body condition of fattening rabbits [39,71,72]. Possible effects of stocking density have been measured using physiological indicators of stress. Higher stocking densities have lead to higher levels of glucocorticoids in hairs and plasma and haematological stress parameters [39,73,74]. However, when using faecal glucocorticoid metabolites or fluctuating asymmetry, no consistent correlation with stocking density has been found [40,71,75]. The behavioral effects of stocking density have also been studied. Several studies report that a higher stocking density will not necessarily lead to negative behavioral effects, as no effect on aggressive interactions as measured by the prevalence of injuries was found [75–79]. In fact, one study found that younger weaned rabbits will freely choose a very high stocking density, huddling close together as they would in a burrow [80]. However, another study found higher stocking densities to lead to an increase in injuries resulting from fights [39]. No clear effect of stocking density on non-aggressive social behaviors has been found either, with one study mentioning no effect [81] and another an increase of social interactions with increasing stocking density [76]. As for non-social behaviors, a lower stocking density clearly leads to an increase in activity [65,75,76,81–86]. Another effect of stocking density on behavior is related to the fattening rabbits' postures. An increase in stocking density has resulted in an increase in sternal lying [77], a resting posture which takes up less space than lateral lying. Similarly, forms of locomotion such as hops and 'playful' jumps are decreased when rabbits have less space available to them [84,87]. Although it has been attempted to measure the effects of stocking density in behavioral tests, often no effects have been found in tonic immobility tests [69,88,89], nor have open field tests lead to consistent findings [69,73,74,88,89].

In sum, stocking density has been shown to be an influence on rabbit welfare. In younger fattening rabbits, decreasing the stocking density may also decrease welfare based on behavioral indicators. A very low stocking density will not allow these rabbits to perform their natural behavior of huddling together in a small space. Older fattening rabbits on the other hand will likely have improved welfare with a lower stocking density. While a higher stocking density does not necessarily lead to an increase in (social) stress, the use of other physiological and behavioral indicators has shown that welfare is likely to be higher in lower stocking densities. Keeping fattening rabbits in cages which allow for comfortable natural movement and postures with the provision of a nest box seems to be the most suitable situation, allowing for adequate responses to social stress caused by stocking density.

Table 3 Experimental designs for examining the effect of stocking density on the welfare of fattening rabbits

Author(s)	Cage size (m^2)	Group size (nr of rabbits)																				
		2	3	4	5	6	7	8	9	10	13	15	16	17	20	26	27	34	40	54	60	100
		Stocking density (rabbits/m^2)																				
Buijs *et al.*, 2011a; 2011b; 2012	0.40							20														
	0.46							17.5														
	0.53							15														
	0.64							12.5														
	0.80							10														
	1.07							7.5														
	1.60							5														
D'Agata *et al.*, 2009	0.26			15.5																		
	1.50							5.5														
Dal Bosco *et al.*, 2002	0.12	16.5																				
	10.23																					10
Hamilton & Lukefahr, 1993	1.85														11				21.5		32.5	
Jekkel & Milisits, 2009; Jekkel *et al.*, 2007; 2008	0.85						8			12	15.5											
Lambertini *et al.*, 2001	1.00							8					16									
Lehmann, 1987	0.18	11																				
Maertens *et al.*, 2004	2.00													8.5				17				

Table 3 Experimental designs for examining the effect of stocking density on the welfare of fattening rabbits

Author(s)	Cage size (m^2)	Group size (nr of rabbits)																				
		2	3	4	5	6	7	8	9	10	13	15	16	17	20	26	27	34	40	54	60	100
		Stocking density (rabbits/m^2)																				
Mbanya *et al.*, 2004	0.42	5		9.5																		
Metz, 1987	0.3				16.5																	
	1.6				3																	
Morisse & Maurice, 1997	0.39					15.5	18	20.5	23													
Paci *et al.*, 2013	0.25			16																		
	0.80			5																		
	1.60			2.5																		
Pinheiro *et al.*, 2012	0.30			13.5																		
	0.53			7.5																		
	80.00														0.25							
Ribikauskas *et al.*, 2010	1.56			2.5																		
	9.00											1.5										
Szendrő *et al.*, 2009	0.50					12		16														
	0.86									11.5	15											
	1.72														11.5	15						
Trocino *et al.*, 2004	0.50							16														
	0.66							12														
Trocino *et al.*, 2008	0.37					16																
	0.50					12																
Trocino *et al.*, 2014; Xiccato *et al.*, 2013	0.11	18																				
	1.68														12		16					
	3.36																		12	16		
Tuyttens *et al.*, 2005	2.00													9				17				
Verga *et al.*, 2004	0.21	9.5	14.5	19																		
Yakubu *et al.*, 2008	0.20	10	15	20	25																	

Group size. The welfare effects of the number of rabbits housed in a single cage or pen (irrelative of stocking density) have also been studied (see Table 4 for range of group sizes tested). Although animals are expected to have a higher risk of disease when living in groups, mortality of group housed fattening rabbits has not been found to be higher when compared to single or pair housed rabbits [68,70,90,91]. No consistent correlation between group size and aggressive interactions has been found. Multiple studies report an increase in aggressive interactions with an increase in group size, as measured by the prevalence of injuries and aggressive behaviors [68,79,92,93]. However, other studies have not found any effects on aggressive interactions [74,90,91,94,95]. One study even found a decrease in aggressive interactions when group size was increased [96]. There are several different factors which could have been responsible for this diversity of results. Different stocking densities have been used by different studies examining the effect of group size. However, some of the studies reporting no effect of group size on aggression have applied greater stocking densities than those finding an increase in aggression. This indicates that stocking density alone cannot explain the variety in results. Age of the study subjects could have been an influence, as fattening rabbits may reach puberty and start establishing a dominance hierarchy near the end of the fattening period [54,97]. The studies reporting an increase in aggression with larger group sizes used later slaughtering ages than those reporting no effects, increasing the chance that their study subjects had already reached puberty. Additionally, a single aggressive individual will likely produce more injuries and attacks when it has access to more group members [98]. It is possible results of increased aggression were caused by a single individual, coincidentally placed in the large group treatment. The sex-composition of a group may also influence the occurrence of aggression. Szendrő and colleagues found that near the end of the fattening period, all-male groups had much higher levels of aggression than all-female or mixed sex groups [99]. Positive social effects of an increase in group size could be explained by the larger surface area available to the larger group of rabbits. An increase in group size at a constant stocking density immediately leads to a larger cage size. As resting rabbits tend to huddle close together, more available space could be created for the active individuals in larger groups. This could reduce social stress, as rabbits are less likely to get in each other's way. This hypothesis has been supported by findings of an increase of positive social interactions and a higher frequency of locomotion activities such as hopping and running in larger groups [42,90,92,95,96,100–102]. This increase in cage size could also account for the higher bone quality found for larger groups of rabbits [96,103,104]. Rabbits in larger groups also appear to be less prone to anxiety as measured in the open field test [100,101], although this result was not always replicated [74].

In sum, the size of a group of fattening rabbits does not appear to have a clear effect on their welfare. No effect on health indicators has been found and behavioral indicators of welfare show no consistent effect on the behavioral patterns performed by fattening rabbits. Positive effects of an increased group size are more likely to be the result of an indirect increase of available space than of the actual number of animals present. Therefore, when attempting to improve the welfare of fattening rabbits, changing their group size is not recommended at the expense of a change in stocking density. However, no welfare studies with fattening rabbits have been found aimed specifically at the possibility of competition over access to feeders and water. This is an aspect of husbandry that seems likely to be correlated directly to group size.

Table 4 Experimental designs for examining the effect of group size on the welfare of fattening rabbits

Author(s)	Cage size (m^2)	Group size (nr of rabbits)																				
		2	3	4	6	8	9	10	12	13	16	18	20	24	26	27	30	40	42	50	54	60
		Stocking density (rabbits/m^2)																				
Combes *et al.*, 2010; Postollec *et al.*, 2008	0.39				15.5																	
	0.66							15														
	4.05																					15
Filiou *et al.*, 2012	0.11	18																				
	0.50						18															
Jekkel *et al.*, 2010	0.85							12		15.5												
	1.70												12		15.5							
Lambertini *et al.*, 2001	0.13	15.5																				
	1.00										16											
Martrenchar *et al.,* 2001	0.39				15.5																	
	1.60													15								
Maertens & van Herck, 2000	0.26			15.5																		
	1.90																16					
Paci *et al.*, 2013	0.80			5																		
	1.60					5																
	3.20										5											
Postollec *et al.*, 2006	0.39				15.5																	
	0.66							15														
	3.67																			13.5		
Dalle Zotte *et al.*, 2009a; Princz *et al.*, 2008a; 2009	0.12	16.5																				
	0.86									15												
Rommers & Meijerhof, 1998	0.35				17																	
	0.70								17													
	1.06											17										
	1.75																17					
	2.50																		17			
	3.23																				16.5	
Szendrő *et al.*, 2009	0.12	16.5																				
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	0.50						18															
Trocino *et al.*, 2014	1.68												12			16						
	3.36																	12			16	
Zucca *et al.*, 2008; 2012a	0.14	14.5																				
	0.21		14.5																			
	0.28			14.5																		

Cage height. A few studies have produced information which helps to discern whether an inability to stand upright is a welfare problem for fattening rabbits. Princz and colleagues housed rabbits in a block of four connected cages, three with a different ceiling height and one lacking a ceiling altogether. The rabbits showed a clear preference for cages with ceilings [105], implying open top cages and pens are not necessary from a welfare perspective. Furthermore, rabbits preferred the highest cage height available to them during the active period and the lowest cage height during the resting period [105]. This could indicate that increasing cage height will allow rabbits to perform more of their natural behaviors. However, one behavioral study using open top pens noted that the upright posture was only rarely performed [96]. Another study comparing the behavior of rabbits in different group sizes observed an increase in the frequency of the upright posture when rabbits were housed in a large group of 50 individuals [90]. Combined, these studies on fattening rabbits suggest that rearing up is used by the rabbits to assess their environment for possible threats. In smaller groups of rabbits housed in cages as fattening rabbits are, the behavior does not appear to be necessary as these rabbits can easily keep an overview of their smaller environment. Based on these behavioral assessments, increasing cage height or using open top cages to enable fattening rabbits to stand fully upright will not lead to an increase of welfare by allowing rabbits to display more natural behaviors. Whether cage height influences welfare through stress has not yet been investigated for fattening rabbits.

Floor type. The welfare studies aimed at the floor type used for fattening rabbit cages have used two main approaches: comparing different types of cage material and/or studying the effects of the presence of bedding material on the cage floor. To investigate the welfare effects of different types of floors irrelative of the presence of bedding, both physiological and behavioral parameters of health and discomfort have been used. When the standard metal wire mesh floor type was compared to a plastic net floor, no effects were found on mortality, bone quality or behaviors performed inside the cage [93,104,106]. However, when given a free choice between these floor types, rabbits show a clear preference for the plastic net floor [92]. Such a preference for floors made from plastic instead of metal wire has also been found in other studies [107–109]. Steel slatted floors have also been studied as a means to improved fattening rabbit welfare. Again, rabbits showed a preference for the steel floors over the standard wire netting [88]. Steel floors do not show an effect on rabbit health as measured by their bone quality, nor do they affect the behaviors rabbits perform inside their cage [88,89]. Hygiene appears to be an important determinant of a rabbit's comfort, as one study found a planked floor (which could easily get soiled with faeces and urine) was least preferred [108]. Another important aspect appears to be the distance between the wires or slats which make up the cage floor. Metal wires with a distance of 14 mm between them and plastic slats with a distance of 16 mm between them hindered the movement of young (pre-weaning) fatteners [110]. When given the choice between floors with or without straw bedding, fattening rabbits prefer to spend their time on floors without bedding [106,107,111–114]. This appears to be related to the hygiene level of the bedding, as rabbits would only spend time on the straw just after it was refreshed [111]. This lack of hygienic conditions could also be the reason for a higher mortality amongst fattening rabbits housed on straw bedding [76]. Lambertini and colleagues suggested straw bedding increases the prevalence of coccidiosis, a digestive disorder. However, only their experimental group with higher stocking density on straw bedding experienced higher mortality [70]. Additionally, Morisse and colleagues found no effects of the presence of straw bedding on the mortality of their rabbits, nor did they record any incidence of coccidiosis [111]. Multiple studies have recorded the behavioral effects of

housing fattening rabbits on straw bedding. However, no consistent findings have been reported. For example, effects reported by different studies on social, comfort and locomotion behaviors have all been contradictory [65,76,81–83,94,111,113]. One positive effect of straw bedding is that it appears to decrease the frequency of stereotypic behaviors [82,113]. This could be due to the fact that rabbits spend time consuming the straw, mimicking their natural extensive foraging behaviors [81–83,87,94,111].

In sum, fattening rabbits appear to experience discomfort from the standard metal wire cage floors they are housed on. This is based entirely on behavioral indicators. Possible health effects of floor type on fattening rabbit welfare have been measured as mortality and bone quality, which were not affected. Also based on behavioral indicators, plastic floors appear to be a suitable replacement of the standard wire netting, as these allow for similar hygienic levels. As for the presence of bedding material, it does not appear to increase the welfare of fattening rabbits. Physiological parameters have shown a decrease in health, while behavioral parameters do not suggest bedding allows for the display of a more diverse behavioral pattern. However, the provision of straw bedding has decreased the performance of abnormal behaviors, a behavioral indicator of stress. Due to the negative health consequences, providing straw in a container such as a rack may provide the positive welfare effects without decreasing hygiene levels.

Enrichment. For fattening rabbits, two main categories of environmental enrichment have been examined: gnawing material and platforms. The effects of enrichment with gnawing material have been studied using physiological and behavioral indicators of welfare. Mortality has been used as a parameter of rabbit health as influenced by the presence of gnawing material. Several studies found no effects [115–117], but one study found an increase in mortality (due to digestive disorders) in a group of rabbits enriched with gnawing sticks when compared to a group enriched with a wire hay rack and a group without enrichment [118]. It was suggested that this was a result from the gnawing sticks becoming unsanitary over time and thereby having an increased contamination with pathogens. No effect on bone quality has been found as a result of gnawing stick presence [104]. The results of the studies on the behavioral effects of enrichment with gnawing material also appear to be mixed. Multiple studies report that rabbits will readily use gnawing sticks and blocks, without showing habituation to them [42,86,92,119–122]. Furthermore, fattening rabbits prefer to have a gnawing stick present in their cage when given the choice [92]. Additional positive effects include less resting (indicating gnawing substrate could be a suitable distraction from boredom) and less aggressive interactions between fattening rabbits [86,92,93,116,123,124]. Some studies have also observed less gnawing on cage bars (considered a stereotypy) and conspecifics when a more suitable gnawing substrate such as a gnawing stick or wooden structure is present [75,77,120,125]. However, it has also been reported that rabbits make very little use of the gnawing stick provided to them [117]. This could have been due to the type of wood used for the sticks, as rabbits have been shown to appreciate certain materials more than others as measured by their use [119,123,124]. Enrichment with gnawing material has not been found to influence the stress response of rabbits as measured by tonic immobility and emergence tests [42,102]. The second common form of enrichment used in welfare studies is a platform structure, which rabbits can use as both elevated extra floor space and as a hiding or resting place when sitting underneath it. When provided with one, fattening rabbits readily use a platform for both purposes [78,95,109,114,126]. Several positive effects have been reported of providing rabbits with a platform. Social interactions between rabbits increased [75,77,95] and stress was reduced as measured by fecal glucocorticoid metabolites [75]. However, fluctuating asymmetry was not influenced by the presence of a platform [71]. No health effects as measured by mortality and injuries have been reported [126]. An

increase in bone quality has been reported when providing fattening rabbits with a platform [103]. However, available space per rabbit was a confounding variable in this study. One study provided both gnawing material and platforms at the same time and found fluctuating asymmetry to be lower in the enriched group of rabbits [40].

In sum, providing enrichment to fattening rabbits appears to be a potential measure to improve their welfare. The numerous studies stating rabbits will readily spend time using enrichment items show that their level of boredom may be reduced. This behavioral finding is supported by reports of lower stress levels in fattening rabbits housed in enriched cages. Deciding on a most suitable type of enrichment item appears to be less straightforward. A platform will likely improve rabbit welfare by increasing the range of natural behaviors that can be performed (such as hiding behaviors) and decrease stress. Also, a platform will provide additional floor space. Although gnawing material has also been shown to be capable of improving rabbit welfare in terms of performed behaviors, this result depends on the material the enrichment item is made of. Also, gnawing material may decrease fattening rabbit welfare through its detrimental effects on health when contaminated with pathogens. Therefore, success of gnawing material provision is likely dependent on the type of item provided, where the material must be suitable for gnawing purposes and contact of the item with faeces inside the cage must be avoided .

Handling. Several studies have studied the effects of regularly handling pre-weaning kits as a means to reduce their fear of human contact. Regular handling of kits has proven to be successful in improving the welfare of fattening rabbits according to both physiological and behavioral indicators. Daily handling of kits reduced their fearfulness as measured by tonic immobility, approach and emergence tests [127,128]. Additionally, kits that were handled daily showed lower mortality and were more often classified as bold based on their behavior in the presence of a human or during an open field test [129–131]. Studies focusing on the timing of the daily handling have shown that there appears to be a sensitive period to the effects of handling around the time of nursing [127,132,133]. Kits that were handled once a day within 30 minutes after nursing during the first week of their life would readily approach a human hand. Kits that were handled several hours after nursing did not show this response. The duration of handling appears to be irrelevant, as even kits that were only touched to check for liveliness instead of picked up out of the nest box and weighed showed an increased performance in the approach test [132]. One study even found similar results for kits that had only been exposed to the smell of a human hand by holding it inside the nest box for five minutes without making physical contact [134].

In sum, regular handling of fattening rabbits will increase their welfare. Rabbits which are accustomed to human contact will not be as fearful during routine handling, are less prone to stress according to behavioral tests and even have better health as measured by mortality. Together, these findings suggest regular handling allows fattening rabbits to cope with regular human contact, which could otherwise be a source of stress.

Transport procedures. The transport of fattening rabbits from their farm to the abattoir has been shown to have a negative impact on welfare, mainly by use of physiological stress indicators. Being transported caused an increase in fecal and plasma glucocorticoid levels [75,135,136] and other haematological parameters related to stress [135–139]. Heart rate and body temperature of fattening rabbits have also been shown to be affected by transport [135]. A longer duration of transport appears

to be related to a further decrease in welfare, as longer transport times have been related to higher mortality and a higher frequency of bruises on resulting carcasses [140,141]. Several studies have attempted to study particular aspects of transport, to determine whether changes could be made to provide a less stressful experience. A study which simulated different stressors experienced during transport found that both high temperature and noise levels increased stress-related haematological parameters [142]. The position of the fattening rabbits on the multi-floor cage used for transport has also been evaluated as a possible influence. Rabbits situated on the bottom level of the multi-floor cage appear to experience more stress than those on higher levels as measured by different stress-related haematological parameters [137,143]. However, this result has not always been replicated [144]. Finally, the way in which the rabbits are loaded onto the truck has been examined. It was found that a rough loading method increases the stress response based on glucocorticoid levels and other haematological parameters as compared to a gentle loading method [138,144]. However, the gently loaded animals also showed an increased stress response compared to those that were not transported [138].

In sum, being transported will decrease the welfare of fattening rabbits irrelative of precautions taken to decrease stress. With current transport procedures (i.e. catching, crating) the rabbits cannot adequately exert control over their situation in order to decrease their fear/stress levels. Furthermore, noise was implicated as a major source of stress, which cannot be avoided when transporting rabbits by truck. Decreasing transport times and employing a gentle loading method will ensure that fear and stress are at least kept to a minimum.

Slaughter procedures. Multiple studies have been aimed at fine-tuning the electrical stunning of fattening rabbits, to ensure that slaughtering itself is not a stressor [145–147]. Based on physiological parameters describing the recovery of fattening rabbits after stunning, it was concluded that electrical stunning is an effective way of producing an unconscious state. Also, electrical stunning appears to be a less stressful stunning method than cervical dislocation, as measured by haematological parameters related to stress [148]. These are relevant findings, as electrical stunning is the most commonly used stunning method. Although electrical stunning can be an effective means of rendering rabbits unconscious, an evaluation of its application in a slaughterhouse has shown that this method was not performed correctly in about 10% of rabbits [48,49]. As a result, these rabbits were still conscious at the time of slaughter. Recently, gas stunning of fattening rabbits has been considered as a possible replacement of electrical stunning. This was suggested to be a possible improvement of the slaughter procedure, since gas stunning does not require the handling of fattening rabbits by abattoir personnel [41,149]. Therefore, this method could be a way to avoid not only stress caused by handling the rabbits, but also incorrect application of electrical stunning. Although gassing rabbits with a mixture of nitrogen and carbon dioxide (20%) produced less behavioral indicators of aversion and respiratory distress than gassing with a higher carbon dioxide concentration (90%), these behaviors were still present more as compared to a sham procedure with atmospheric air [41]. One study showed that gas stunning produced a physiological stress response which was not only higher than that of control animals which were not stunned or slaughtered, but also higher than that of rabbits slaughtered without stunning [149]. This indicates that both electrical and gas stunning have their specific effects on the welfare of fattening rabbits. Whereas electrical stunning, when applied correctly, produces immediate unconsciousness, it requires physical handling of the rabbits which could induce fear. Gas stunning appears to be a source of stress in itself, whereas no handling is required. As fattening rabbits can be accustomed to regular handling,

electrical stunning has the potential of being relatively stress free. It is unlikely that the sensation of choking that is produced by gas stunning will cease to be a source of stress. Therefore, from a welfare point of view, electrical stunning is preferred.

Pre-slaughter lairage is another common aspect of fattening rabbit slaughter. Increasing the duration of lairage time has been suggested as a means of decreasing post-transport stress levels [143]. However, other studies have reported a decrease in welfare due to increased lairage time as measured by both haematological parameters of stress and mortality [140,141,150]. As lairage includes further handling of fattening rabbits and mixing with unfamiliar animals in another unfamiliar environment, it is unlikely a suitable means of decreasing post-transport stress levels. In combination with the detrimental effects on health, increasing lairage time will not be in the fattening rabbits' best interest.

3.2 Breeding rabbits

The main purpose of breeding rabbits is to produce offspring. Certain practices are common to both bucks and does being used as breeding stock. Breeding rabbits are housed individually [45](Figure 3A/D). Standard cages are constructed of metal wire [45,151]. Enrichment is usually not provided and breeding rabbits are often fed exclusively on pellets. The use of plastic foot mats is becoming more and more frequent for breeding does [45]. Also, does are at least periodically group housed, as they are kept together with their kits from parturition until weaning [151](Figure 3B). The does are provided with a nest box, in which they construct a nest of fur and any additionally provided nesting material, such as straw [152]. From birth until weaning, does have free access to their nest and are unable to close the nest entrance [153]. After weaning, either the doe, the kits or both are moved to a new cage [45]. The reproductive rhythm applied to the breeding doe can be described as intensive (rebreeding occurs immediately after parturition), semi-intensive (rebreeding occurs during lactation) or extensive (rebreeding occurs after weaning). A semi-intensive reproductive rhythm, with rebreeding 10 days after parturition, is most common [154]. Artificial insemination is the most common means of fertilization [45,46](Figure 3C). As for the breeding males, they are kept individually for long periods of time [45](Figure 3D). There are now specialized semen collection centers, which house only breeding males [155].

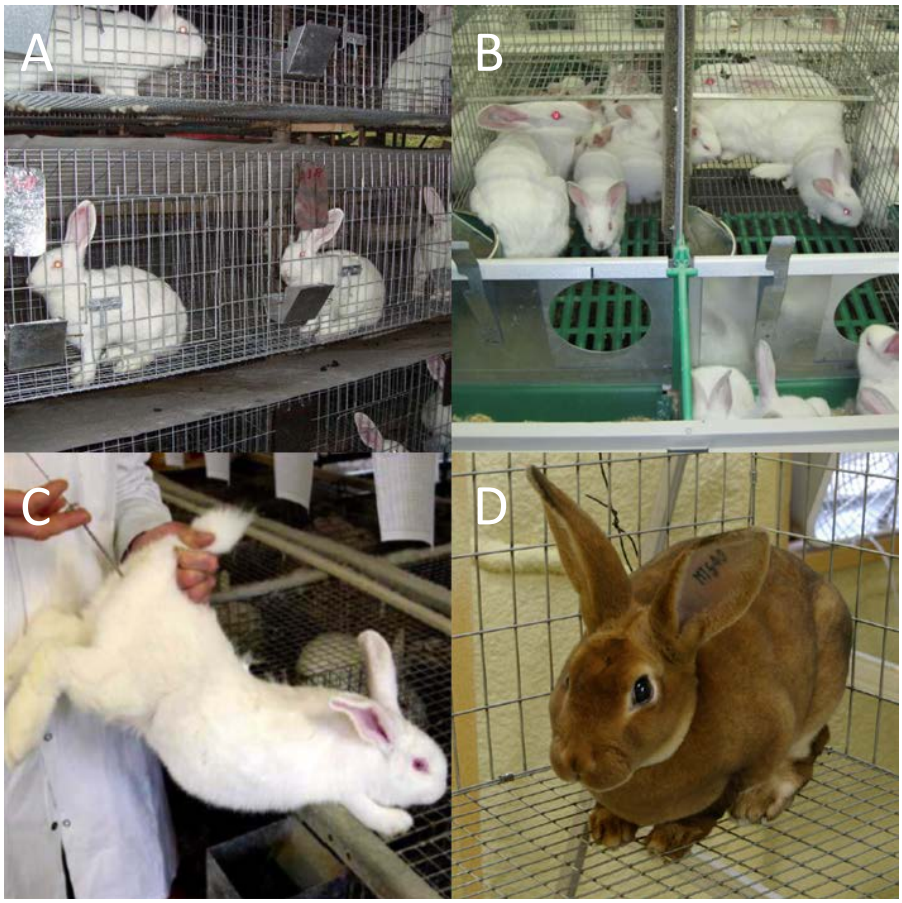

Figure 3 Common aspects of breeding rabbit husbandry, with individual housing of breeding does (A), breeding does housed with pre-weaning kits (B), artificial insemination (C) and individual housing of breeding bucks (D).

3.2.1 Welfare problems

The following practices form potential threats to the welfare of breeding rabbits:

- **Health problems.** Both female and male breeding rabbits spend their entire life indoors, in an artificial environment created for them. Factors such as air quality and hygiene could negatively affect their health status. Additionally, breeding does could suffer from decreased health as a result of the reproductive rhythm that is imposed on them.
- **Weaning.** In the wild, maternal care is very limited for rabbits [28]. Under common breeding practices, does are forced to be in close contact with their kits from parturition until weaning. This unnatural behavior pattern could be a source of stress when the doe cannot adequately respond by removing herself from the vicinity of her kits. Additionally, does do not have the ability to close off their nest, a behavior which is always performed in the wild [28].
- **Housing conditions**, including:
    - **Cage size.** The size of the cages breeding rabbits are housed in could limit comfortable resting and movement, similar to the effects of stocking density in fattening rabbits.
    - **Cage height.** See welfare problems fattening rabbits (3.1.1).
    - **Floor type.** Although floor mats are commonly provided, most of the floor space available to breeding rabbits still consists of metal wires. This could be a source of discomfort and injury. Floor mats are typically not large enough for the rabbits to be able to perform patterns of locomotion on them, restricting their ability for comfortable movement.
    - **Individual housing.** Both bucks and does lack the ability to perform social interactions with other adult rabbits. This could be of particular importance to the welfare of breeding does, as female rabbits are very social in the wild [28]. Although bucks are known to occasionally lead solitary lives, it is more common for them to be part of a social group. Therefore, their welfare could also be affected by individual housing.
    - **Enrichment.** See welfare problems fattening rabbits (3.1.1).
- **Handling.** See welfare problems fattening rabbits (3.1.1).

3.2.2 Welfare studies

The following possible welfare problems for breeding rabbits have received scientific attention (see Table 5 for overview):

Health problems. Breeding rabbits are susceptible to various health problems. Amongst both does and bucks, respiratory disorders have a high prevalence [46,52,155,156]. Similar to fattening rabbits, breeding does and bucks also suffer from digestive disorders [155]. Mastitis (infection of the mammary glands) was found to be a common ailment of breeding does [46,156,157]. A main cause of mastitis is bacterial infection. These findings imply that improving the hygiene of the housing of breeding rabbits will have a positive impact on their welfare, by possibly decreasing the prevalence of

Table 5 Overview of studies on breeding rabbit welfare.

Welfare problem(s)	Welfare indicator(s)	N	Age (weeks)	Study duration (weeks)	Sex	Author(s)
Health problems						
General health status - surveillance on farms	Disease occurrence	-	-	-	f/m	Rosell, 2003
General health status, reproductive rhythm – individual health checks on farms	Body condition, disease occurrence	3751	-	-	f	Rosell & de la Fuente, 2008
General health status - surveillance on farms	Body condition, disease occurrence	-	-	-	f/m	Rosell & de la Fuente, 2009a
General health status - surveillance on farms	Disease occurrence	-	-	-	f/m	Rosell *et al.*, 2009
General health status - surveillance on farms	Body condition, disease occurrence	-	-	-	f	Sanchez *et al.*, 2012
Reproductive rhythm, **weaning age** – interval between parturition and artificial insemination	Energy balance	246	-	1[1]	f	Feugier & Fortun-Lamothe, 2006
Reproductive rhythm – interval between parturitions	Body condition, mortality	122	16.5	31.5	f	Gerencsér *et al.*, 2011
Reproductive rhythm – interval between parturition and remating	Energy balance	89	21	1[1]	f	Parigi Bini *et al.*, 1996
Reproductive rhythm, **weaning age** – interval between parturition and remating	Energy balance	96	-	1[1]	f	Xiccato *et al.*, 2004a
Reproductive rhythm, **weaning age** – interval between parturition and artificial insemination	Energy balance	96	-	1[1]	f	Xiccato *et al.*, 2005
Pre-weaning conditions						
Weaning age	Energy balance	108	-	1[1]	f	Xiccato *et al.*, 2004b
Open nest box – presence of cat flap at nest entrance	Behavioral observation, plasma glucocorticoid level, mortality (kits)	30	16	4[1]	f	Baumann *et al.*, 2005b
Open nest box, **cage size** – presence of tunnel at nest entrance	Behavioral observation	30	-	1[1]	f	Selzer *et al.*, 2004
Housing conditions						
Cage size - all cages included plastic floor mats	Behavioral observation	60	11	10	f	Bignon *et al.*, 2012b
Cage size – non-pregnant and pregnant/lactating does	Preference test	19	-	1 (non-pregnant does) /4 (pregnant does)	f	Mikó *et al.*, 2012b
Cage size, **floor type** – bigger cages included plastic foot mat	Fecal glucocorticoid level	252	16	4[1]	f	Prola *et al.*, 2013
Floor type – presence of plastic foot mat	Injury occurrence (foot injuries)	-	-	-	f	de Jong *et al.*, 2008
Floor type – presence of plastic foot mat; larger cages included plastic platform	Injury occurrence (foot injuries), mortality	108	16.5	-	f	Mikó *et al.*, 2012c

Floor type – presence of plastic foot mat	Cleanliness of cage floor, injury occurrence (foot injuries)	-	-	-	f	Rommers & de Jong, 2011
Floor type – presence of plastic foot mat	Disease occurrence, injury occurrence (foot injuries)	224	8	52	f	Rosell & de la Fuente, 2009b
Individual housing – regrouping with familiar or unfamiliar group members	Behavioral observation (agonistic interactions), fecal glucocorticoid level, injury occurrence (aggression)	96	34	-	f	Andrist *et al.*, 2012
Individual housing – surveillance of group housing on farms	Injury occurrence (aggression)	-	-	-	f	Andrist *et al.*, 2013
Individual housing, **cage size** – group housing with training of does to recognize a nest box as their own	Behavioral observation	-	52	3[1]	f	Dal Bosco *et al.*, 2004
Individual housing – regrouping in novel or familiar pen	Behavioral observation, body temperature, injury occurrence (aggression)	104	30	-	f	Graf *et al.*, 2011
Individual housing – group housing with or without training of does to recognize a nest box as their own	Behavioral observation, injury occurrence (aggression)	24	-	3[1]	f	Mugnai *et al.*, 2009
Individual housing, **enrichment** – group housing with or without individual territory establishment, straw and/or hiding places	Behavioral observation, injury occurrence (aggression)	200	-	5[1]	f	Rommers *et al.*, 2014
Individual housing, **reproductive rhythm** – group housing, group housed does had access to hay and straw; interval between parturition and artificial insemination	Behavioral observation, faecal glucocorticoid level, kit mortality	50	17	27.5	f	Szendrő *et al.*, 2013
Enrichment, **cage height**, **floor type** – presence of platform; cages with platform had raised ceilings; presence of floor mat	Behavioral observation	12	-	2[1]	f	Alfonso-Carrillo *et al.*, 2014
Enrichment - presence of platform	Kit mortality	58	-	-	f	Barge *et al.*, 2008
Enrichment – presence of gnawing block	Behavioral observation, gnawing block consumption, mortality	80	-	5	f	Bignon *et al.*, 2012a
Enrichment – wood shavings or straw as nest material	Preference test	60	-	1[1]	f	Blumetto *et al.*, 2010
Enrichment - presence of birch twigs or onion bulbs	Disease occurrence, injury occurrence (aggression), mortality	90	35	55	f/m	Gugolek *et al.*, 2008
Enrichment – presence of long straw in trough or short trough in metallic container	Behavioral observation	26	-	3	f	López *et al.*, 2004
Enrichment – presence of gnawing blocks made of different materials	Behavioral observation, gnawing block consumption, mortality	105	-	1[1]	f	Maertens *et al.*, 2012
Enrichment – presence of gnawing blocks made of different materials	Behavioral observation, gnawing block consumption, mortality	105	-	1[1]	f	Maertens *et al.*, 2013
Enrichment – presence of nesting material	Behavioral observation	14	56-68	4.5	f	Metz, 1987
Enrichment, **floor type** – presence of platform; platform were made of metal wire or plastic	Behavioral observation	31	16.5	5[1]	f	Mikó *et al.*, 2012a
Handling						
Handling - durability of reduced fear	Approach test, open field	28	4	20	-	Pongrácz &

towards humans displayed by regularly handled rabbits	test, novel object test					Altbäcker, 1999 - experiment 3

Welfare problem(s) Possible rabbit welfare problem(s) examined in study with short description of experimental manipulations. *Welfare indicator(s)* List of indicator(s) used to measure rabbit welfare. *N* Number of study subjects used for experiment. *Age* Age of study subjects at start of experiment. *Study duration* Duration of experimental treatment. *Sex*: *f* female/doe, *m* male/buck. *Author(s)* Researcher(s) responsible for experiment. [1] = study duration in reproductive cycles.

common diseases. However, this has not yet received scientific attention. Apart from the incidence of diseases, an important reason for the culling of breeding rabbits is poor body condition [155]. A factor which negatively influenced the body condition of breeding does was their reproductive rhythm (the interval between parturition and next mating/artificial insemination) [157,158]. Several studies have focused on the relationship between the reproductive rhythm of does and their energy balance. All found that a longer interval between parturition and subsequent artificial insemination improved the does' health by having a less negative impact on their energy balance [159–162]. Also, as does progress through multiple kindlings, both their body condition and the prevalence of respiratory disorders increases [156]. Similarly, survival of does rapidly decreases with multiple kindlings, with a higher mortality for does undergoing an intensive reproductive rhythm [163]. Together, these studies indicate that a more extensive reproduction rhythm will increase the welfare of breeding does by improving their health.

In sum, several different health problems amongst breeding rabbits appear to be caused by the sanitary status of their housing. This implies breeding rabbits are not able to adequately avoid infection with disease by removing themselves from likely sources of pathogens. Improving air quality and cage hygiene could be possible means of improving the welfare of breeding rabbits, however, the effects of such alterations have not yet been studied. For breeding does, applying an extensive reproduction rhythm will allow them to adequately respond to the physical demands of pregnancy and lactation by maintaining better energy reserves.

Weaning. Through regular husbandry practices, does often spend a lot more time around their kits than would occur in the wild. As kits have more and longer access to their mother, they have the possibility to (attempt to) nurse more frequently than their wild counterparts. This has been shown to have repercussions on both the doe's health and her behavior [164]. First of all, the age at which kits are weaned has been shown to influence the doe's body condition and energy balance. Weaning the kits at a later age will decrease the doe's body condition [159] and increase her energy deficit [161,162,165]. Breeding does' behavior also implies a negative influence on their welfare from the unnatural amount of contact with their kits. For example, it has been reported that when a platform is available in the doe's cage, she will start using it more when the kits start leaving the nest box to explore the rest of the cage [109]. Then, when the kits start to use the platform as well, the doe's frequency on the platform decreases again. A similar finding was reported by Alfonso-Carrillo and colleagues, who also provided breeding does with a platform. They found the peak in the does' platform use coincided with their regular nursing period. In combination with other behavioral indicators (such as an increase in hyperactive behaviors for does with kits), this implies breeding does will actively attempt to get away from their kits when they are nearing their weaning age [166]. This could be interpreted as a breeding doe's preference for housing without the constant presence of kits near weaning age. Several attempt have been made to decrease the contact between doe and kits prior to weaning. By using a tunnel as an entrance to the nest box, the kits are not as obviously

present to the doe as they are when an open nest box is used. This has been shown to decrease nursing activity of the doe [167]. The same was found for an increase in cage size, possibly due to the allowance of a greater distance between the doe and her nest [167]. A similar study used a cat-flap to simulate a closed nest-entrance, as would be the case in the wild [168]. This study found that closing the nest box decreased the does' stress levels as measured by glucocorticoid levels. Additionally, these does made less potentially disturbing visits to the nest, thereby decreasing pup mortality.

In sum, the current practice of housing kits in open nest boxes within the doe's cage until weaning decreases the welfare of breeding does. Open nest boxes will limit the doe's ability to perform natural behavior patterns, such as closing the nest entrance. This has been shown to be a cause of stress for the does and poor health for the kits. Additionally, weaning age influences the health of breeding does in a way similar to reproductive rhythm. Does' energy reserves are decreased when kits remain with the doe until a later weaning age. Additionally, behavioral indicators have shown that the does experience stress from the constant presence of the kits. Providing a more natural situation by simulating a closed nest and weaning kits at an earlier age will likely benefit the welfare of both breeding does and kits.

Cage size. The impact of cage size on the welfare of breeding rabbits has only been studied for breeding does (see Table 6 for range of cage sizes tested). When they are given the choice between cages of different sizes, breeding does show a preference for a larger cage [169]. This preference was particularly pronounced during the does' active period. The effect of a larger cage size on the performance of abnormal behaviors is unclear. One study found no effect on stereotyped behaviors such as bar gnawing and self-grooming [170]. Another found that does in smaller cages performed more stereotypies [171]. However, this study compared the effects of cage size and group housing simultaneously, making it unclear whether cage size was responsible for the decrease in abnormal behaviors. A consistent finding seems to be that does are not only more active in larger cages [170,171], they also take on a larger range of postures [171]. This finding seems intuitive, as small cages could easily restrict postures which take up more space. As for the health effects of larger housing, only one study considered the mortality of their study subjects and found cage size to have no effect [170]. Finally, rabbit does in larger cages have been found to have lower fecal glucocorticoid concentrations [172], indicating they have lower stress levels.

In sum, providing more floor space will increase the welfare of breeding does. It allows them more comfort as evidenced by the larger range of postures displayed by does in larger cages. Also, does in larger cages are more active and are less likely to experience stress.

Table 6 Cage sizes used for examining the effect of cage size on the welfare of breeding does.

Author(s)	**Cage sizes tested (surface area in m^2)**		
Bignon *et al.*, 2012b	0.12	0.23	0.34 + 0.09 (platform)
Dal Bosco *et al.*, 2004*	0.23		1.14
Mikó *et al.*, 2012b	0.22		0.44
Prola *et al.*, 2013	0.32		0.52

*Confounding variable: group housing

Cage height. Only one study has examined the possible welfare effects of an increased cage height for breeding rabbits. When breeding does were housed in cages which allowed a fully upright position, this behavior was only rarely observed [166]. Based on this one study, it can be concluded that increasing the cage height will not make a tremendous impact on breeding rabbit welfare.

Floor type. The possible welfare threat posed by metal wire floors has received a fair amount of scientific attention. That such floors can actually decrease the welfare of breeding rabbits has been shown by the prevalence of foot injuries in both does and bucks. Ulcerative pododermatitis or 'sore hocks', a condition in which the soles of the rabbit's feet become raw and inflamed, is a common occurrence amongst the breeding stock of rabbit farms [46,155–157]. This welfare problem seems to be preventable, as foot injuries are less prevalent when foot mats were provided to breeding does [156,173–176]. These mats ensure that breeding rabbits do not have to spend all of their time in contact with the metal wiring of their cage floor. Additional evidence for a welfare improvement through foot mats have been provided by other welfare indicators. When a foot mat is available, breeding does will spend most of their time on the mat instead of the cage floor [166], indicating active avoidance of the metal wiring. Also, breeding does housed in cages with a foot mat showed a decreased fecal glucocorticoid concentration [172]. Several studies have also studied the effects of changing the entire cage floor instead of improving it only partially by providing a foot mat. When the metal wires making up the cage floor were thickened from the standard 2 mm to 3.02 mm, no effect on the prevalence of foot injuries was found [173]. Changing the floor material from metal wire to plastic mesh does appear to be an improvement, as breeding does housed on those floors showed a lower prevalence of foot injuries [174]. Additionally, when breeding does are provided with a platform inside their cage, they will spend more time on it when it is made of plastic mesh than when it is made of metal wires [109].

In sum, all of these results suggest that the current standard housing with metal wire mesh floors are a negative influence on the welfare of breeding rabbits. This practice leads to discomfort and injuries, as has been shown by both physiological and behavioral welfare indicators. Although the provision of a foot mat allows breeding rabbits to avoid contact with the metal wire floor, this does not provide a means for comfortable locomotion. Therefore, substituting the metal wire with plastic netting is considered a further improvement of the welfare of breeding rabbits.

Individual housing. The possibility of housing breeding rabbits in groups has only been investigated for breeding does (see Table 7 for range of group sizes and stocking densities studied). This has led to both positive and negative welfare effects of group housing being reported. First of all, group housing breeding does will lead to a wider and more natural behavioral repertoire, as the rabbits can now perform social interactions [171,177]. This increase in social behaviors came paired with a decrease in stereotypies [171,177,178]. However, it is not only positive social interactions which increase when breeding does are housed in groups. Multiple studies report an increase in agonistic interactions and injuries resulting from them [163,177–179]. Additionally, group housed does have higher stress levels as measured by fecal glucocorticoid levels and higher mortality than individually housed does [163]. Although these results suggest that social housing is more likely to worsen a breeding doe's welfare status than to improve it, this is not necessarily the case. According to the definition of good welfare, the breeding does should be able to adequately respond to being housed in a group. This response

will include the establishment of a dominance hierarchy, which will be accompanied by agonistic interactions [32]. The most important determinant of the welfare effect of group housing will be whether the breeding does have an improved welfare status after they have established a dominance hierarchy. One study reported that although aggression amongst breeding does initially increased when they were housed together, does started performing positive social interactions once a hierarchy had been established [171]. A complication for group housed breeding does is that they are temporarily separated from their group for parturition, leading to a constantly repeated establishment of a dominance hierarchy. Because of this, increased aggression after regrouping breeding does has been reported [179,180]. Several ways of avoiding this obstacle to group housing have been tested. Regrouping does in an unfamiliar, 'neutral' territory does not appear to be a solution, as it had no effect on the duration and frequency of aggressive interactions [181]. In fact, the does which were regrouped in the group's familiar home pen were found to have fewer injuries and lower stress as measured by body temperature [181]. Similar findings are reported by Andrist and colleagues, who reported that regrouping does with a stable, familiar group led to a decrease in injuries and stress as measured by fecal glucocorticoid metabolites [180]. Perhaps maintaining a stable group could lead to a stable dominance hierarchy which persists even when individual animals are temporarily removed and introduced back into the group again. Another approach is to cease separating breeding does from their group altogether. Mugnai and colleagues housed does in group cages which were provisioned with multiple nest boxes. Does that were trained to recognize a nest box as their own showed fewer agonistic interactions and more positive social interactions [177]. This could also improve the welfare of kits, as multiple does using the same nest box when group housing has been suggested as the main reason for a higher kit mortality [163]. When breeding does know their group mates and their own territory within the cage, this could lead to more successful group housing.

Table 7 Experimental designs for examining the effect of group housing on the welfare of breeding does (cage sizes include next boxes)

Author(s)	**Cage size (m^2)**	**Group size (nr of rabbits)**				
		1	4	5	5-7	8
		Stocking density (rabbits/m^2)				
Andrist *et al.*, 2012	5.7					1.5
Dal Bosco *et al.*, 2004	1.52		2.5			
Graf *et al.*, 2011	5.8				1	
Mugnai *et al.*, 2009	0.24	4				
	1.52		2.5			
Rommers *et al.*, 2014	1.54		2.5			
Szendrő *et al.*, 2013	0.32	3				
	7.7			0.5		

In sum, group housing of breeding does is likely the most effective way of enabling a more natural behavioral repertoire, thereby increasing their welfare. Although group housing leads to temporary increases of aggression and social stress, a decrease in welfare could be avoided by allowing breeding does to adequately respond to their group members by establishing a dominance hierarchy

and giving them the space to avoid each other when necessary. This is supported by physiological and behavioral measures of stress declining when groups stabilize over time. When housed individually, breeding does have no means of adequately responding to their isolation. Therefore, this would be considered a more serious threat to their welfare than the possibility of negative social interactions.

Enrichment. Similar to group housing, the welfare effects of enrichment on breeding rabbits has only been studied for breeding does. Possible applications of environmental enrichment have been studied for both individually and group housed does. As for individually housed breeding does, enrichment with gnawing material, straw and a platform have been studied. The results of enrichment with gnawing material are mixed. Although breeding does will readily make use of a suitable gnawing substrate [115,116,122,182], no effects on abnormal behaviors such as bar gnawing have been found [115,182]. An interesting find is that breeding does enriched with a gnawing block showed a reduced frequency of nest box visits [122,182]. As frequent nest box visits could have a detrimental effect on both the health of kits and the stress levels of the doe, this implies keeping breeding does busy with enrichment materials could improve the welfare of both parties. The success of such a strategy could be dependent on the material which is used as a gnawing substrate, as breeding does have been shown to have a preference amongst different types of gnawing blocks [122]. Providing does with straw in a container as environmental enrichment seems to be unsuitable. Two different studies have reported that does have little long-term interest in this form of enrichment [178,183]. Several studies provided breeding does with a platform inside their cage. It was reported that the does spent a significant amount of their time using the platform [109,166]. During their active period, does used the platform as extra floor space, whereas they mainly used it as a shelter during their resting period. Also, a platform could reduce the stress experienced by does due to the constant presence of their kits [166,184]. Does have been shown to use a platform to escape from their kits once they leave the nest box and start competing with her for available space [166], while the provision of a platform caused kit mortality to decrease in another study [184]. One study investigated the effects of environmental enrichment on group housed does. When does were provided with straw, no effects on aggressive interactions were found. However, provision with hiding places (such as a platform) reduced the frequency of injuries resulting from aggressive interactions [178]. Finally, a type of enrichment typical for breeding does is nest material. One study compared the suitability of different types of nest material in a preference test [185]. 95% of the tested does did not remove the provided additional nest material, but used it in combination with their fur to create a nest for their kits. When given a choice between straw and wood shavings, a vast majority of the does chose to use a nest box with straw.

In sum, enrichment with gnawing materials allows for more natural behaviors to be performed by breeding does. However, no clear effect on behavioral indicators of stress has been found. The effect of gnawing items could be dependent on the material from which they are made, as breeding does show a preference for specific materials. Providing breeding does with a platform will also likely improve their welfare. It provides an opportunity for natural hiding behaviors, thereby allowing the rabbits to adequately respond to fear-inducing stressors. Additionally, it allows breeding does to distance themselves from their kits, further simulating a more natural situation. This has led to welfare improvement as measured by behavioral indicators and physiological indicators of social stress. Finally, provision of nest material appears to be preferred by breeding does, although this conclusion is based on a single behavioral study.

Handling. Although not specifically aimed at breeding rabbits, one study has produced results which indicate regular handling could improve their welfare. This study found that when kits are handled daily during the first week of their life (with handling times as short as 3 minutes per litter), they will be less fearful of humans and maintain this lack of fear into adulthood [133]. This suggests that handling future reproductive stock will have a long-lasting positive effect on their welfare, as they will have to be handled regularly in adulthood. Accustoming future breeding rabbits to this feature of their captive lives will decrease the fear they experience as adults.

3.3 Laboratory rabbits

Laboratory rabbits may experience different stressors depending on the experiments they are used for. However, there are some common aspects of life as a laboratory animal which are experienced by most, if not all, laboratory rabbits. First of all, laboratory rabbits are often housed individually in small cages, usually made of sheet metal or metal wire [186](Figure 4A). These cages are often barren, lacking environmental enrichment [187]. In order to keep track of experimental treatments and results, laboratory rabbits have to be individually identifiable. This is usually accomplished by tattooing a number in their ears. Irrelative of the experimental purpose of the laboratory rabbit, it will be regularly handled and restrained during its life [186](Figure 4B&C). This is particularly true for transgenic rabbits, whose blood and/or milk have to be regularly collected.

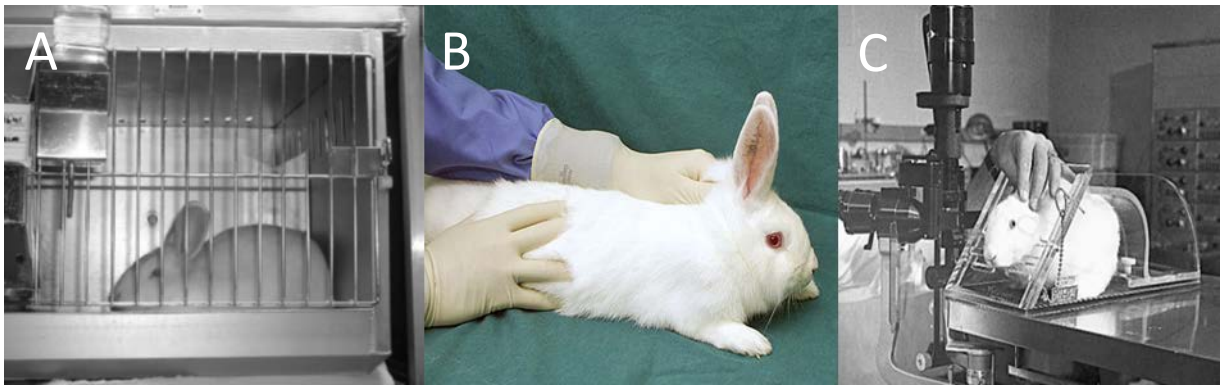

Figure 4 Common aspects in laboratory rabbit husbandry, with individual housing (A), handling (B) and restraining (C) of rabbits.

3.3.1 Welfare problems

The following practices form potential threats to the welfare of laboratory rabbits:

- **Housing conditions**, including:
    - **Cage size.** See breeding rabbits (3.2.1).
    - **Individual housing.** See breeding rabbits (3.2.1).
    - **Stocking density.** See fattening rabbits (3.1.1).
    - **Enrichment.** See fattening rabbits (3.1.1).
- **Handling.** See fattening rabbits (3.1.1).
- **Laboratory procedures.** The different uses of laboratory rabbits all form a possible threat to their welfare. Surgical procedures are a potential source of pain, as are the drugs tested on laboratory rabbits. These could also be a source of discomfort, depending on their application. Restraint of laboratory rabbits (e.g. during examination, collection of plasma or milk) could be a similar, but increased, source of stress compared to handling. Additionally, individual identification of laboratory rabbits could also be painful, depending on the method.

3.3.2 Welfare studies

The following possible welfare problems for laboratory rabbits have received scientific attention (see Table 8 for overview):

Cage size. Although laboratory rabbits are often housed individually, only a few studies have investigated the possible welfare effects of increasing cage size (see Table 9 for cage sizes tested). When observing the behavior of laboratory rabbits in standard cages, it was reported that movement is restricted [188,189]. This implies standard cages are not large enough to allow for the comfortable performance of a natural behavioral repertoire. This finding is supported by studies comparing the behavior of individually and pair or group housed laboratory rabbits. When housed in pairs or groups, the rabbits' available space doubled. This led to a general increase in locomotion [187] and an increase in specific forms of locomotion such as hopping and running [190]. Another study reported that rabbits that were individually housed show more abnormal behaviors in a smaller cage [191]. This is an interesting result, as a decrease in available space is expected to limit the rabbits in their behavioral repertoire, possibly leading to discomfort and stress. Unfortunately, no studies have measured the effects of cage size on welfare using indicators other than behaviors.

In sum, providing laboratory rabbits with larger cages will likely improve their welfare. Behavioral indicators have shown that standard cages do not allow for an adequate response to discomfort (as movement is restricted) or stress (as abnormal behaviors are performed).

Table 8 Overview of studies on laboratory rabbit welfare.

Welfare problem(s)	Welfare indicator(s)	N	Age (weeks)	Study duration (weeks)	Sex	Author(s)
Housing conditions						
Cage size, **individual housing** – larger cages contained bedded flooring; group housing	Behavioral observation	18	12	2	f	Krohn *et al.*, 1999
Individual housing - 24 hour isolation period	Body temperature, faecal and plasma glucocorticoid level, heart rate	10	7	1[1]	f/m	Baias *et al.*, 2012
Individual housing, **cage size** – pair housing; pairs were housed in larger cages	Behavioral observation	12	9	21	f	Chu *et al.*, 2004
Individual housing – group housing	Behavioral observation (aggression), haematological parameters, plasma glucocorticoid level	6	-	16	f	Fuentes & Newgren, 2008
Individual housing, **cage size** – housing in standard laboratory cages	Behavioral observation	18	-	25	f/m	Gunn & Morton, 1995
Individual housing, **enrichment** - group or individual housing in enriched environment	Behavioral observation (agonistic interactions), preference test	18	-	20[2]	f	Held *et al.*, 1995 - experiment 1
Individual housing, **enrichment** - group housing in enriched environment or individual housing in barren environment	Behavioral observation (agonistic interactions), preference test	9	-	20[2]	f	Held *et al.*, 1995 - experiment 2

Individual housing – group housing in enriched environment	Behavioral observation	36	-	30[3]	f	Held *et al.*, 2001
Individual housing - pair housing of castrated or intact males	Behavioral observation, injury occurrence (aggression)	24	12	-	m	Kalagassy *et al.*, 1999
Individual housing - group housing	Behavioral observation	-	8-9	-	f	Love & Hammond, 1991
Individual housing - pair housing with familiar or unfamiliar conspecific	Behavioral observation, heart rate, plasma glucocorticoid level	38	12	20	m	Noller *et al.*, 2012
Individual housing – group housing	Behavioral observation	47	-	12	f/m[4]	Podberscek *et al.*, 1991a
Individual housing, **enrichment** – possibility for limited social contact; presence of platform	Motivation test, preference test	11	22-27	2	f	Seaman *et al.*, 2008
Stocking density – change in group size	Haematological parameters, plasma glucocorticoid level	90	5	6	f/m	Onbasılar & Onbasılar, 2007
Stocking density – change of cage size	Behavioral observation (social interactions)	22	-	2[2]	f	Valuska & Mench, 2013
Enrichment - presence of hay on top of wire cages, half of the cages were also enriched with a platform	Behavioral observation	86	16-31 [3]	2[3]	f/m	Berthelsen & Hansen, 1999
Enrichment – presence of mirror	Preference test	74	5	6	f/m	Dalle Zotte *et al.*, 2009b
Enrichment - presence of mirror	Behavioral observation	24	15-16	2	f/m	Edgar & Seaman, 2010
Enrichment - presence of platform	Behavioral observation, open field test	96	11-25[3]	6[3]	f/m	Hansen & Berthelsen, 2000
Enrichment - presence of a single type of toy or food item	Behavioral observation	18	7	2	f/m	Harris *et al.*, 2001
Enrichment - presence of a toy	Behavioral observation	48	-	8	f/m	Johnson *et al.*, 2003
Enrichment - presence of a single type of enrichment item	Behavioral observation	60	13	4	m	Lidfors, 1997
Enrichment - presence of a single type of enrichment item	Behavioral observation	13	8	12	m	Poggiagliolmi *et al.*, 2011
Handling						
Handling - repeated handling by familiar and unfamiliar people	Behavioral observation, handling test	14	6-30[3]	1[3]	f/m[4]	Podberscek *et al.*, 1991b
Handling - daily handling of adult rabbits	Behavioral observation, handling test	21	20	3	f	Swennes *et al.*, 2011
Handling, **individual housing** – daily handling; effect of neutering	Approach test, behavioral observation (social interactions), body temperature, open field test, novel object test, tonic immobility test	40	0	17	m[4]	Verwer *et al.*, 2009
Laboratory procedures						
Post-operative pain	Behavioral observation	7	>12	-	m	Farnworth *et al.*, 2011

Post-operative pain - treatment with analgesic	Behavioral observation	28	14	3[1]	f	Leach *et al.*, 2009
Individual identification tattoo - treatment with local anaesthetic cream	Behavioral observation, facial expression, heart rate, plasma glucocorticoid level	8	-	-	f/m	Keating *et al.*, 2012
Individual identification microchip	Injury occurrence (implant site)	5	12-26	8	f/m	Mrozek *et al.*, 1995
Use of flux-controlled chamber	Behavioral observation	10	1-5	1[1]	f	Olivas *et al.*, 2013

Welfare problem(s) Possible rabbit welfare problem(s) examined in study with short description of experimental manipulations. *Welfare indicator(s)* List of indicator(s) used to measure rabbit welfare. *N* Number of study subjects used for experiment. *Age* Age of study subjects at start of experiment. *Study duration* Duration of experimental treatment. *Sex*: *f* female/doe, *m* male/buck. *Author(s)* Researcher(s) responsible for experiment. [1] = study duration in days, [2] = study duration in number of trials, [3] = age or study duration in months, [4] = castrated males.

Table 9 Cage sizes used for examining the effect of cage size on laboratory rabbit welfare.

Author(s)	**Cage size(s) tested (surface area in m^2)**	
Gunn & Morton, 1995	0.30	
Hansen & Berthelsen, 2000	0.35	
Krohn *et al.*, 1999	0.28	0.56

Individual housing. Housing laboratory rabbits without access to conspecifics appears to be cause of stress. Individually housed adult rabbits perform abnormal behaviors [188]. Additionally, individually housed rabbits prior to puberty have higher glucocorticoid levels compared to group housed rabbits [38]. Multiple efforts have been made to study the applicability of group housing to laboratory rabbits (Table 10). Most of these studies have been aimed at female rabbits. It has been suggested that adult does are more affected by social deprivation as they displayed more abnormal behaviors derived from social grooming (such as chewing and licking their own fur) compared to bucks [188]. Several other behavioral studies have shown that does appear to appreciate social contact with conspecifics. In a motivation test, Seaman an colleagues assessed how female rabbits, housed individually in barren cages, value different additions to their environment. These rabbits were most motivated to work for limited social contact, where they could interact with another rabbit through a wire mesh barrier [192]. Additionally, it has been observed that rabbits housed in pairs will spend most of their time in physical contact with each other, even though there is enough space in the cage for them to be out of each other's reach [187]. Group housing also appears to be beneficial for the stress levels of laboratory rabbits, as they have been observed to perform less abnormal behaviors [187,190,191,193]. However, group housing could also cause aggressive interactions between rabbits, which could decrease their welfare if they cannot adequately respond to their conspecifics. Agonistic interactions have been observed between group housed female laboratory rabbits [187,194]. However, positive social interactions such as social grooming and play have also been reported [194]. One study examined the feeding behavior of pair housed rabbits, to evaluate any possible competition over access to food. It was found that both the dominant and subordinate rabbits spend equal times feeding, indicating competition was not a problem [187]. Held and colleagues gave laboratory rabbits a free choice between group and solitary housing. A rabbit was placed in a start box from which she could either join her group or enter an empty pen, identical in size and enrichment features. It was found that the rabbits were slightly more likely to enter the empty pen, rather than enter the pen which contained the other rabbits [195]. When the empty pen on offer was smaller and barren, rabbits

Table 10 Experimental designs for examining the effect of group housing on the welfare of female laboratory rabbits.

Author(s)	Cage size (m^2)	Group size (nr of rabbits)								
		1	2	3	4	6	7	10	14	20
		Stocking density (rabbits/m^2)								
Chu *et al.*, 2004	0.46	2								
	0.93		2							
Fuentes & Newgren, 2008	0.25	4								
	8.91			0.5						
Held *et al.*, 2001	3				1.5					
Krohn *et al.*, 1999	0.28	3.5								
	0.56	2								
	3.5					1.5				
Podberscek *et al.*, 1991a	0.20	5								
	1.84						4			
	3.14								4.5	
	8.16									2.5
Verwer *et al.*, 2009*	3.5							3		

*Group-housed neutered males.

did show a clear preference for group housing. The initial preference for solitary housing was explained by the authors as a consequence of rabbits' natural behavior, which consists of resting in company while active behaviors are usually performed at more of a distance from conspecifics. This could have influenced their results, as the rabbits were active during testing and therefore possibly less inclined to join their group [195]. Only one study has used a physiological welfare indicator to assess the effects of group housing adult female laboratory rabbits. This study reported not observing any aggression amongst group members, nor did group housed rabbits show an increased stress response as measured by glucocorticoid levels [196].

Very little research is aimed at the group housing of male laboratory rabbits. One study has shown that housing bucks in an unstable social environment leads to continued agonistic interactions and physiological signs of chronic stress such as a continued increase of glucocorticoid level [197]. When housed in a stable social environment (by being paired with a littermate), bucks showed less agonistic and more affiliative interactions, indicating that social housing could be beneficial to the welfare of male rabbits as well. This was further supported by individually housed bucks showing increased physiological signs of stress (heart rate) as compared to the bucks which were housed socially with their littermates. However, this result could also have been due to general inactivity and/or boredom. It has been suggested that neutering may be an effective way of reducing aggressive interactions between group housed male rabbits [198,199]. Castrated pairs of male litter mates have been successfully housed together, whereas intact males would develop aggression during puberty [198]. However, no studies have investigated whether groups of neutered males have improved welfare compared to those housed individually or in mixed-sex groups.

In sum, providing female laboratory rabbits with social contact will improve their welfare. Based on behavioral indicators, rabbits have a need for social contact and when this need is not met, it is a source of stress. When housed individually, laboratory rabbits cannot adequately respond to this

need for social interactions, as there are no appropriate substitutes for conspecifics present within their environment. Although there is mention of agonistic social interactions between laboratory rabbits, this is not a welfare problem as long as the rabbits can adequately respond to each other's presence by establishing a dominance hierarchy. This appears to be possible for female rabbits based on behavioral and physiological parameters of social stress. As for male laboratory rabbits, both physiological and behavioral indicators suggest their welfare is threatened by individual housing. However, there is not enough scientific data to suggest a suitable solution for this welfare problem. Housing intact males in groups leads to continued agonistic interactions, possibly because an all-male group is not a natural occurrence for rabbits [28]. Housing with litter mates and castration have been suggested as improvements, as these options have been shown to decrease the frequency of agonistic interactions.

Stocking density. Two studies have examined the effects of stocking density on the welfare of group housed laboratory rabbits (Table 11). It was found that a higher stocking density will increase the stress experienced by the rabbits as measured by glucocorticoid levels [200]. This effect was more pronounced in male laboratory rabbits. Also, it was found that when pairs of does were first introduced to each other in a larger cage, this reduced the occurrence of aggression as measured by injuries [201]. Therefore, welfare of group housed laboratory rabbits can be improved by decreasing stocking density, as this will increase their ability to adequately respond to their conspecifics.

Table 11 Experimental designs for examining the effect of stocking density on the welfare of female laboratory rabbits.

Author(s)	**Cage size (m^2)**	**Group size (nr of rabbits)**			
		1	2	3	5
		Stocking density (rabbits/m^2)			
Onbasılar & Onbasılar, 2007	0.42	2.5		7	12
Valuska & Mench, 2013	0.91		2		
	1.44		1.5		

Enrichment. For laboratory rabbits, the effects of enrichment with multiple different items have been studied. The need for environmental enrichment has been shown by the behavioral patterns of laboratory rabbits housed in a standard barren cage. These rabbits spend most of their time being inactive and commonly display stereotypies [188]. Enriching their cages with hay (by placing the hay on top of the cages, so the rabbits could pull it into their cages) reduced the frequency of bar gnawing and excessive grooming [202]. A similar results was found for laboratory rabbits who received one of four different types of items as enrichment. When provided with hay in a plastic bottle or grass cubes, the rabbits performed less abnormal behaviors [203]. Also, the rabbits spent more time interacting with those enrichment items than with boxes or gnawing sticks. Such a preference for food-related enrichment items was replicated in a study by Harris and colleagues, who also found their rabbits to spend more time interacting with such items as opposed to different types of non-edible toys [204]. One study provided both degradable (made of fruit flavored cardboard) and non-degradable (made of sturdy plastic) toys. They found both types of toys to be readily used by the laboratory rabbits, with rabbits spending more time chewing on their toy than on their cage [205]. A study providing their rabbits with a stainless steel toy found that while the rabbits were initially interacting with it quite frequently, this interest decreased significantly over the following weeks [206].

Apparently, not all enrichment items reach the desired effect of providing a long-term distraction. Laboratory rabbits have also received platforms as an enrichment item. These appear to be able to improve their welfare, as a motivation test found that rabbits will work for access to a cage with platform [192]. Once they could actually reach the platform though, they were rarely observed on top of it, making it seem as though it is a platform's additional function as hiding place which makes it attractive. Another study found that it was the female rabbits in particular who used a platform for the shelter it provided [189]. However, all rabbits in this study were more frequently seen on top of their platform than underneath it. Rabbits from enriched cages were described as being less restless than those from barren cages based on the number of behavioral transitions performed in their cage and during an open field test [189]. Finally, the effects of enrichment with mirrors have been investigated for laboratory rabbits. Only behavioral indicators were used, and it was found that mirrors may provide a sense of social contact as younger rabbits of both sexes prefer to be housed in cages enriched with mirrors [207]. As for adult laboratory rabbits, mirrors appear to be a potential substitute for social contact for female rabbits as the presence of a mirror decreased the frequency of self-grooming [208]. For the male rabbits, no clear effect of the presence of mirrors was found. It is possible that mimicking the presence of another male rabbit by placing a mirror inside their cage does not improve the welfare of male rabbits, as male-male positive social contact is not common for unfamiliar adult rabbits [28].

In sum, the barren environment provided by cages lacking enrichment form a welfare problem for laboratory rabbits. Adding enrichment items has been shown to increase welfare by reducing the performance of behavioral indicators of stress. Based on the different types of enrichment items used, it seems that degradable food-related items could be preferable over items such as gnawing sticks or toys, which may quickly lead to habituation. Also, providing laboratory rabbits with a platform could increase welfare by enabling a wider range of natural behaviors, which the rabbits seem to prefer. Finally, mirrors are a potential form of social enrichment for individually housed female laboratory rabbits based on behavioral indicators of stress and preference.

Handling. As laboratory personnel do not always have the chance to habituate laboratory rabbits to human handling during their sensitive period (before being weaned), several studies have investigated the effects of regular handling on adult rabbits. It was found that regular handling can quickly reduce the fearfulness of adult laboratory rabbits towards humans, as measured by their behavior while being handled [209,210]. Furthermore, regularly handled male laboratory rabbits were described as having a more pro-active coping style during different behavioral tests, suggesting they were less prone to anxiety [199]. Therefore, regular positive contact with humans is recommended to improve the welfare of laboratory rabbits by reducing their fear of being handled.

Laboratory procedures. Although the procedures that laboratory rabbits undergo as part of different studies may vary greatly, several studies have examined the welfare effects of certain common procedures. Firstly, tattooing rabbits in the ears for individual identification causes pain as measured by parameters such as behavior, facial expression, heart rate and blood pressure [43]. When rabbits were provided with a local anesthetic cream, they displayed none of these indicators of pain, suggesting its use could enhance the welfare of laboratory rabbits [43]. Micro-chips (which are injected under the skin) have been suggested as an alternative method of individual identification [211]. However, the response of laboratory rabbits to this method have not yet been evaluated. Abdominal surgery was also found to be a cause of pain in both male and female laboratory rabbits based on

their behavioral response [212,213]. It was concluded that the common low dosages or lack of analgesia provided post-surgery are not conducive to good rabbit welfare, as they could be experiencing post-operative pain [213]. Finally, the possible welfare effects of placing laboratory rabbits inside flux-controlled chambers (commonly used in animal research) have been examined. Although rabbits display an increase of behaviors suggesting alertness after being placed inside the chamber, no further behavioral indicators of stress were observed [214].

In sum, pain caused by laboratory procedures is likely a welfare problem for laboratory rabbits based on behavioral and physiological indicators. Their coping with pain could be more successful by administering suitable dosages of analgesia and/or anesthetic.

3.4 Pet rabbits

There is a large amount of variety in the non-commercial rearing of pet rabbits [215]. For example, a wide variety of accommodations are available for pet rabbits, from small indoor hutches to large outdoor constructions (Fig. 5). The social environment of pet rabbits also varies greatly, from being housed alone to pair housing with a conspecific or a member of another species of pet animal [215]. Different types of feed for pet rabbits are available on the market [216], allowing for possible differences in adequacy of nutrition. Finally, even though the frequency and duration of handling may differ, all pet rabbits are regularly exposed to contact with humans.

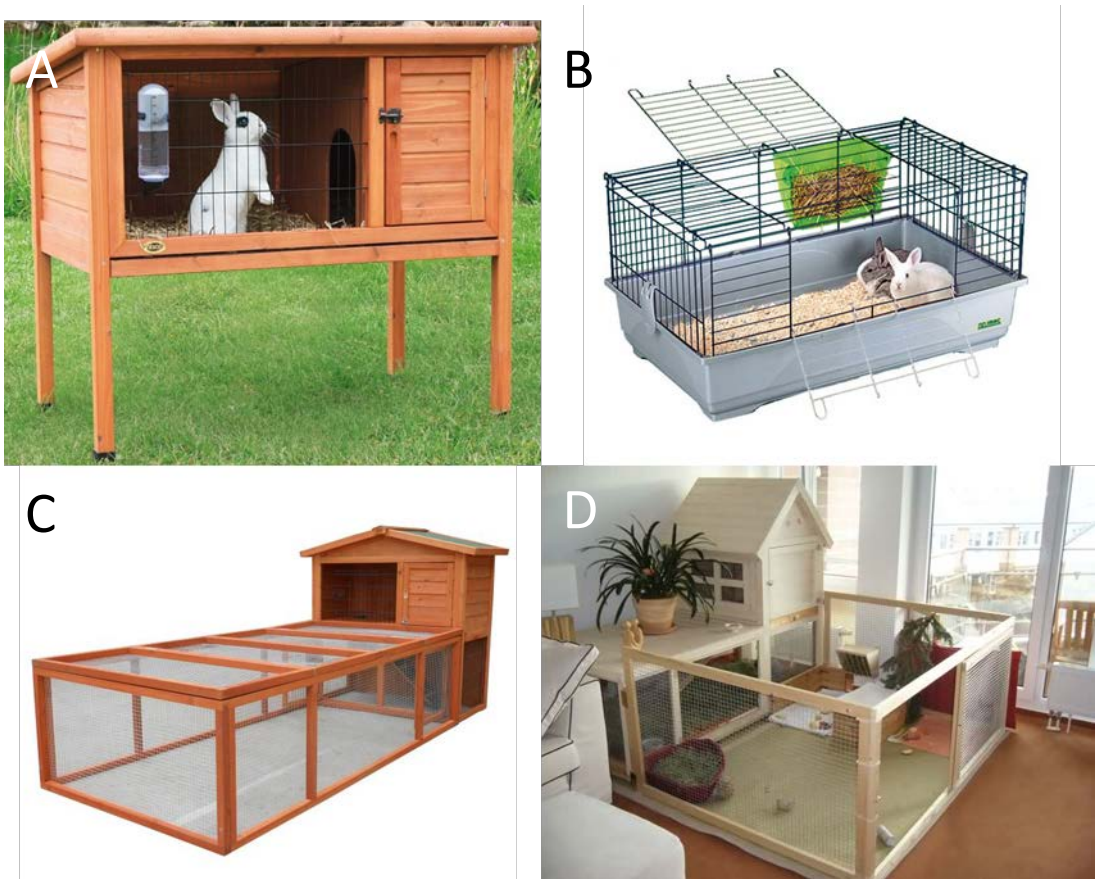

Figure 5 Housing for pet rabbits, with standard commercially available outdoor (A) and indoor (B) hutches, and custom made outdoor (C) and indoor (D) enclosures.

3.4.1 Welfare problems

The following practices form potential threats to the welfare of pet rabbits:

- **Health problems.** As the use of pet rabbits is not physically taxing, they are expected to have a higher life expectancy than other categories of rabbits. Their health is dependent upon the supervision and expertise of their owners.
- **Housing conditions**, including:
    - **Cage size.** See breeding rabbits (3.2.1).
    - **Individual housing.** See breeding rabbits (3.2.1).
    - **Enrichment.** See fattening rabbits (3.1.1).

- **Handling.** See fattening rabbits (3.1.1).

3.4.2 Welfare studies

The following possible welfare problems for pet rabbits have received scientific attention (see Table 12 for overview):

Health. Knowledge about the health status of pet rabbits is available through owner surveys and records of veterinary clinics. From these sources, it appears that pet rabbit owners do not have sufficient knowledge of common rabbit ailments. This could be a possible explanation for the relative rarity of older pet rabbits [215]. For example, most pet rabbits are not neutered, despite the fact that neutering may prevent uterine diseases in does and behavioral problems in both does and bucks [215,217]. Additionally, dental disease was found to be prevalent amongst pet rabbits, often without the owner's awareness [215,218,219]. Dental problems are more common for pet rabbits housed in hutches than those that are allowed to range free in the garden [218]. The causes of dental problems are not yet fully understood, however, nutrition and abnormal teeth wear have been suggested as possible influences [218–220]. It was found that pet rabbits are selective feeders, picking out only preferred items from their commercial rabbit feed. The items that were least popular with pet rabbits were those that contain the necessary nutrients for healthy dental development [220]. Furthermore, it was suggested that proper digestion (stimulated by sufficient dietary fiber levels) will enhance the uptake of these necessary nutrients. These findings all suggest that pet rabbits may suffer from decreased welfare due to improper nutrition. The prevalence of obesity was found to be low amongst pet rabbits [215,217]. However, whether this is due to sufficient exercise or insufficient nutrition remains unclear.

In sum, health problems may pose a threat to the welfare of pet rabbits. Letting diseases and injuries go untreated because they are not recognized could limit the rabbit's adequate response to its health condition. The above results also suggest that pet rabbits are not provided with adequate food. Although the low prevalence of obesity may suggest that the nutritional value of pet rabbit food is adequate, the high prevalence of dental disease suggests that it is lacking in nutrients required for normal tooth development. This indicates pet rabbits are not free to adequately respond to incorrect food.

Cage size. Several studies have examined the effect of cage size on the welfare of pet rabbits (Table 13). Based on surveys amongst pet rabbit owners, most pet rabbits are housed in hutches placed in the owner's garden [215,221]. Hutches that are categorized as being small (<0.34 m^2) were used by 20 percent of respondents who provided information about the size of their rabbit's housing [221]. It was suggested that many of the respondents were 'keen' pet owners, striving to provide good care of their rabbit. Therefore, it seems likely that this study was biased towards rabbits housed in larger hutches. This indicates that small housing could be a relevant welfare problem for pet rabbits. This is supported by a motivation study in which pet rabbits were required to work for access to additional available space. It was shown that rabbits were motivated to work for access to the largest available cage size, more so than for a medium sized addition to their housing [222]. Furthermore, when the costs for this increase in living space were increased (by requiring more work from the rabbits), locomotion behaviors such as hops were performed more frequently once access to the extra space was acquired. This rebound effect suggests that pet rabbits are motivated to perform such bouts of

Table 12 Overview of studies on pet rabbit welfare.

Welfare problem(s)	Welfare indicator(s)	N	Age (weeks)	Study duration (weeks)	Sex	Author(s)
Health problems						
Obesity - survey among companion animal practices	Disease prevalence	141	-	-	f/m	Courcier *et al.*, 2012
Dental disease - questionnaire on diet filled in by pet rabbit owners	Behavioral observation, disease prevalence	90[1]	-	-	f/m	Harcourt-Brown, 1996
Dental disease - questions on housing conditions answered by owners	Disease prevalence	81	-	-	f/m	Harcourt-Brown & Baker, 2001
Dental disease - survey among veterinary hospital patients	Disease prevalence	105	1-5[2]	-	f/m	Mosallanejad *et al.*, 2010
General health, **dental disease**, **individual housing**, **cage size** - survey among pet rabbit owner's homes	Behavioral observation, body condition, disease prevalence	102	12-416	-	f/m	Mullan & Main, 2006
Housing conditions						
Cage size	Behavioral observation, motivation test	?	-	-	-	Dixon & Cooper, 2010
Cage size - response to a change in cage size	Behavioral observation	19	17-360	6	f/m	Dixon *et al.*, 2010
Cage size, **individual housing**, **general health** - questionnaire filled in by pet rabbit owners	-	52[1]	-	-	f/m	Edgar & Mullan, 2011
Enrichment - access to grass pasture	Behavioral observation, motivation test, preference test	16	11-16	-	f	Leslie *et al.*, 2004
Handling						
Handling, **individual housing**, **cage size** - survey among pet rabbit owner's homes	Behavioral observation, handling test	102	12-416	-	f/m	Mullan & Main, 2007

Welfare problem(s) Possible rabbit welfare problem(s) examined in study with short description of experimental manipulations. *Welfare indicator(s)* List of indicator(s) used to measure rabbit welfare. *N* Number of study subjects used for experiment. *Age* Age of study subjects at start of experiment. *Study duration* Duration of experimental treatment. *Sex*: *f* female/doe, *m* male/buck. *Author(s)* Researcher(s) responsible for experiment. [1] = N in number of questionnaires, [2] = age in years.

active locomotion [222]. Similar findings are reported in another study by Dixon and colleagues, where rabbits also increase the frequency of active locomotion after being moved from a small to a large enclosure [223]. This same study found rabbits to be more interactive in larger enclosures. An increase in interaction with their environment (measured as playing behaviors) was also found for rabbits which had access to a run or were allowed to roam free periodically [224].

In sum, smaller cage sizes affect pet rabbit welfare by limiting their ability to perform natural behaviors such as active locomotion and play behaviors. Also, larger cages are likely to improve the welfare of pet rabbits as they have shown a behavioral preference for them.

Table 13 Cage sizes used for examining the effect of cage size on the welfare of pet rabbits.

Author(s)	**Cage size(s) tested (surface area in m^2)**		
Dixon & Cooper, 2010; Dixon *et al.*, 2010	0.88	1.68	3.35
Edgar & Mullan, 2011	<0.34	0.34-0.68	>0.68
Mullan & Main, 2006	0.20-1.24		

Individual housing. A survey amongst pet rabbit owners has shown that pet rabbits are often housed individually [221]. No studies have yet been performed to compare the welfare of individually and pair or group housed pet rabbits.

Enrichment. One study examined whether pet rabbits' welfare could be improved by allowing them access to a grass pasture [225]. It was found that when given a choice between grazing on grass or eating commercial feed, pet rabbits have a preference for grass. However, in a subsequent motivation test, no clear difference in response was found. The initial preference for grass could be explained by its novelty, which had worn off by the time of the motivation test. Also, the study subjects were fed with hay in addition to their feed, meaning they had access to a suitable chewing substrate, even when grass was not available to them. Based on this study, access to a grass pasture for grazing is not necessary for good rabbit welfare.

Handling. To date, a single study has observed welfare effects of human handling on pet rabbits. Rabbits which were handled frequently by their owners struggled less while being handled than those which are not handled regularly [224]. This indicates pet rabbits habituate to being handled when it is performed frequently, possibly reducing the stress experienced by these rabbits. Therefore, regular handling could improve the welfare of pet rabbits.

3.5 Angora rabbits

Angora rabbits used for wool production have an average productive longevity of 3-4 years [226]. During this time, they are housed in such a way that the quality of their fur remains as high as possible (i.e. without stains or matting)[227]. To this end, Angora rabbits are usually housed in cages made of concrete and wire which lack any bedding material (Figure 6A)[12]. Another important aspect of Angora rabbit husbandry is the collection of their fur. Their hairs are removed by different methods, after which the rabbits grow it back and the procedure repeats (usually around 4 weeks after harvesting). Methods of collection include clipping the hairs (Figure 6B), shearing the hairs (Figure 6C) and plucking the hairs (6D). Prior to plucking, a defleecing agent may be added to the rabbit's diet to promote natural hair loss [12]. All of these methods usually include the restraint of the Angora rabbit. Wool resulting from plucked Angora hairs is considered superior in quality to wool spun from clipped/shorn hairs [227].

Figure 6 Common aspects in Angora rabbit husbandry, with individual housing in wire cages (A) and different methods of wool collection [clipping (B), shearing (C) and plucking (D)].

3.5.1 Welfare problems

It is important to note that Angora rabbits are not always kept for the purpose of wool collection. They are also a popular ornamental breed. Here, only those possible welfare problems that are directly related to wool production are discussed. For welfare threats related to their use as ornamental rabbits (i.e. due to their physical appearance), see paragraph 3.6.

The following practices form potential threats to the welfare of Angora rabbits:

- **Health problems.** After their hairs have been removed for the production of wool, Angora rabbits are housed in barren cages with no or very short fur. This could threaten their health and comfort as their body temperature could drop due to excessive heat loss [227].
- **Housing conditions**, including:
    - **Cage size.** See breeding rabbits (3.2.1).
    - **Floor type.** See fattening rabbits (3.1.1).
    - **Individual housing.** See breeding rabbits (3.2.1).
    - **Enrichment.** See fattening rabbits (3.1.1).
- **Handling.** See fattening rabbits (3.1.1).
- **Fur collection.** The removal of an Angora rabbit's fur could be a welfare problem of varying magnitude, depending on the means of collection. Restraining rabbits (by their ears or by tying their legs) is a potential source of discomfort, fear and pain. Furthermore, the plucking of hairs without a defleecing agent is very likely to decrease rabbit welfare, as it is a painful procedure from which the rabbits cannot escape.

3.5.2 Welfare studies

Health problems. It has been suggested to provide Angora rabbits with woolen jackets for 2-3 weeks after wool has been collected to prevent heat loss [227]. Also, maintaining strips of fur along the back or providing a nest box could allow the rabbit to maintain a suitable body temperature [12]. One study has investigated the effectiveness of both suggestions (Table 14). Both rabbits wearing jackets and those with a remaining strip of fur maintained a higher body temperature than rabbits which were plucked completely and did not receive a jacket [228]. However, the rabbits wearing jackets showed a change in their regular behavior pattern, indicating they were experiencing discomfort. Therefore, leaving a strip of fur seems to be the most suitable solution to prevent heat loss in Angora rabbits after wool collection.

Table 14 Overview of studies on Angora rabbit welfare.

Welfare problem(s)	Welfare indicator(s)	N	Age (years)	Study duration (days)	Sex	Author(s)
Health problems						
Heat loss after wool collection – leaving a strip of fur on the back or wearing a woolen jacket	Behavioral observation, body temperature	23	1-3	2	-	Vermorel *et al.*, 1988

Welfare problem(s) Possible rabbit welfare problem(s) examined in study with short description of experimental manipulations. *Welfare indicator(s)* List of indicator(s) used to measure rabbit welfare. *N* Number of study subjects used for experiment. *Age* Age of study subjects at start of experiment. *Study duration* Duration of experimental treatment. *Sex*: *f* female/doe, *m* male/buck. *Author(s)* Researcher(s) responsible for experiment.

3.6 Ornamental rabbits

The husbandry of ornamental rabbits is very similar to that described for breeding rabbits (see paragraph 3.2), with individual housing in cages. Therefore, most of the welfare problems encountered by ornamental rabbits have already been discussed. However, there are several breeds of ornamental rabbits which have been suggested to experience poor welfare as a result of selection for traits which are part of their breed's standard [229]. Spotted rabbit breeds, such as the English spot and Checkered Giant (Fig. 7A), are bred for their distinctive body markings. Angora breeds (also used for wool production, see paragraph 3.5) are bred for their long coats of hair (Fig. 7B). Dwarf breeds, such as the Netherland dwarf, are selected for their body type. They have compact, rounded bodies with a relatively large, round head (Fig. 7C). Last, for the lop breeds, such as the French lop and English lop, their ears are their most prominent feature (Fig. 7D). These should be long and droopy, hanging down the side of the rabbit's head.

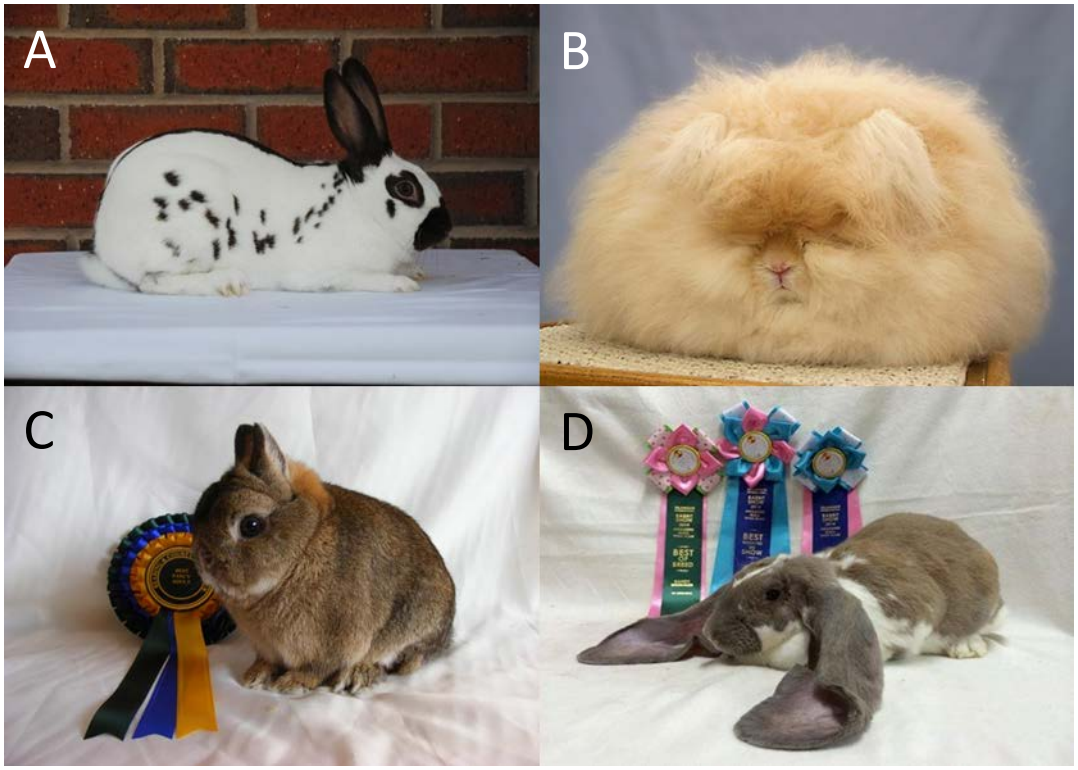

Figure 7 Ornamental breeds that are suspected of having inherent welfare problems, with spotted (A), Angora (B), dwarf (C) and lop (D) rabbits used for exhibition purposes.

3.6.1 Welfare problems

The following traits of specific ornamental breeds of rabbits form potential threats to their welfare:

Spotted breeds. The desired spotted coat of these breeds is the result of a heterozygous genotype for the Dominant white spotting allele [230]. Rabbits that are homozygous for the dominant allele are susceptible to colon disorders.

Angora breeds. A possible threat to the welfare of Angora rabbits bred for exhibition purposes is posed by their long hair. Their coat could cause discomfort by increasing body temperature and by

limiting their sight. Additionally, Angora rabbits could ingest hairs when grooming [229]. It is also possible the welfare of Angora rabbits is more severely threatened by unhygienic housing conditions, as their longer hairs are more likely to come into contact with soiled surfaces inside their cage. This could lead to increases susceptibility to conditions such as skin infection and fly strike (where flies lay their eggs on the rabbit's soiled fur, leading to maggot infestation)[231].

Dwarf breeds. Dwarf rabbits are not simply a smaller version of standard/large breeds. Rather, their skull has a different shape, with a relatively shorter and broader face [232]. Due to the shape of their skull, dwarf rabbits could be susceptible to dental problems such as malocclusion. This could limit their ability to feed. Additionally, it has been suggested that dwarf rabbits are prone to tear duct problems [229].

Lop breeds. The long ears which are desirable in lop rabbits could also threaten their welfare. When their ears are long enough to reach the ground, comfortable locomotion could be limited. Also, their ears are then more prone to injury [229].

3.6.2 Welfare studies

The following possible welfare problems for pet rabbits have received scientific attention (see Table 15 for overview):

Spotted breeds. Rabbits which are homozygous for the Dominant white spotting allele are likely to develop a so-called megacolon, where the colon dilates due to obstipation [230,233]. The condition limits proper functioning of the rabbit's digestive system, thereby reducing the welfare of these rabbits by causing discomfort and disease. It has been shown that homozygous rabbits for the dominant allele are more likely to develop a megacolon and have a higher mortality than rabbits which are heterozygous for the spotting gene [233]. As the symptoms of hereditary megacolon syndrome are not present in all predisposed homozygous rabbits [230], it is possible that factors other than genetics could influence the occurrence and development of the disease.

Angora breeds. The only study of Angora rabbit welfare found was focused on the ingestion of hair as a possible welfare problem. It was concluded that the ingestion of hair by Angora rabbits is a cause of trichobezoar formation, a type of hair ball that combines with stomach contents inside the stomach. Out of all the deaths for a population of Angora rabbits, almost a quarter were caused by trichobezoars [234]. Based on this study, hair ingestion poses a threat to the welfare of Angora rabbits by reducing their health. Perhaps this problem could be avoided by regular grooming, thereby reducing the amount of hair which the rabbit could ingest.

Table 15 Overview of studies on ornamental rabbit welfare.

Welfare problem(s)	Welfare indicator(s)	N	Age (weeks)	Study duration (weeks)	Sex	Author(s)
Spotted breeds						
Megacolon syndrome	Disease prevalence	50	0	10	-	Fontanesi *et al.*, 2014
Megacolon syndrome	Disease prevalence, mortality	105	0	21	f/m	Wieberneit & Wegner, 1995

Angora breeds						
Hair ingestion	Disease prevalence, mortality	560	-	5[1]	f/m	Mondal *et al.*, 2006

Welfare problem(s) Possible rabbit welfare problem(s) examined in study with short description of experimental manipulations. *Welfare indicator(s)* List of indicator(s) used to measure rabbit welfare. *N* Number of study subjects used for experiment. *Age* Age of study subjects at start of experiment. *Study duration* Duration of experimental treatment. *Sex*: *f* female/doe, *m* male/buck. *Author(s)* Researcher(s) responsible for experiment. [1] = study duration in years.

4. Discussion

The present review provides an overview of the current knowledge of welfare problems faced by different categories of domestic rabbits. This overview was created with the main aim of providing future directions for domestic rabbit welfare research. By reviewing the welfare status of multiple categories of domestic rabbits, it can be concluded that there are many welfare problems encountered by domestic rabbits. Although some are specific for their own category, many of these welfare problems and their suggested improvements can be applied to domestic rabbits in general. For these common welfare problems, suggestions are provided for the improvement of domestic rabbit welfare. Also, suggestions for future research are given when even this combined knowledge is not sufficient as a basis for welfare recommendations.

It is important to view the following recommendations for welfare improvement and suggestions for future research within the context of the limitations of the current review. First of all, the scope of welfare studies that it has been based on was limited by the availability of studies. It is unlikely all relevant welfare studies were found. However, every effort was made to include as many studies of domestic rabbit welfare as possible. It has recently been suggested that animal welfare scientific literature is suffering from several forms of publication bias [235]. For example, welfare studies reporting an improvement of animal welfare in their experimental groups are published more than those reporting no difference or a negative effect of experimental treatment. It is possible that domestic rabbit welfare studies show a similar positive result bias. Therefore, it is possible suggestions for future research have already been produced, but have not been published due to a lack of positive results. Next, not all categories of reared domestic rabbits were included as part of this review. For example, domestic rabbits are also reared for the production of pelts or as (live) food for large carnivores housed in zoos [1]. By excluding these categories from this review, any welfare studies related to them have not been discussed. Finally, the definition of good welfare used for this review represents an unrealistic situation when compared to the conditions of domestic rabbits reared in captivity. Therefore, captive conditions are more likely to be deemed a threat to welfare using this definition than would have been the case when using a definition with lower welfare demands. However, the aim of this review was not to compare the relative severity of different welfare problems faced by domestic rabbits. Rather, the identification of possible welfare problems and suggestions for their improvement was considered valuable to the encouragement and guidance of future research aimed at domestic rabbit welfare. Using a definition of good welfare which covers a broad spectrum of demands decreased the chance of overlooking possible welfare problems.

4.1 Welfare suggestions based on combined knowledge

Several possible welfare problems have been studied for different categories of domestic rabbits. Combining the knowledge gathered by these studies will benefit all categories of rabbits involved and will prevent redundant research efforts. By combining these separate research efforts, suggestions for the improvement of domestic rabbit welfare can be made which are based on a combination of different welfare indicators, increasing the validity of these suggestions.

Health problems. Welfare studies aimed at the improvement of frequent health problems have been produced for fattening rabbits, breeding rabbits and pet rabbits. In order to achieve good

rabbit welfare, rabbits must be housed in an environment where they can avoid unnecessary disease or injury [15]. The fact that several categories of domestic rabbits are faced with common health problems caused by husbandry indicates that adequate housing in terms of the third freedom is not yet the case for many rabbits. Understanding the causes of these health problems could be relevant to all domestic rabbits, as it could lead to a better understanding of how to prevent these problems. Studies with fattening rabbits, breeding rabbits and pet rabbits have all shown the potential welfare improvement associated with the provision of forage that is high in fiber content (such as hay). A lack of dietary fiber has been shown to be the cause of digestive disorders and resulting mortality in fattening rabbits [57,236,237]. These digestive disorders have also been found to be a common occurrence in breeding rabbits [155]. Additionally, pet rabbits commonly suffer from dental diseases, which has been suggested to be due to a lack of access to appropriate nutrients or insufficient uptake of them through unsuccessful digestion [215,218–220]. Together, these findings suggest that when domestic rabbits do not have access to a suitable fiber source, their welfare will be threatened. They will not have the freedom to adequately respond to incorrect food or disease. Additionally, providing domestic rabbits with hay will allow for the display of a more normal behavior pattern. In the wild, rabbits spend most of their active time foraging [28]. Providing roughage such as hay will allow domestic rabbits to spend more time on feeding behaviors as compared to when they only have pellets available to them. This advice is supported by findings of straw consumption by fattening rabbits housed on straw bedding [81–84,94,111] and successful enrichment of laboratory rabbits with hay [202,203].

Another important finding related to domestic rabbit health is the importance of keeping the rabbits' environment hygienic. Common diseases amongst breeding rabbits, such as respiratory diseases and mastitis, are caused by a poor sanitary status [46,156,157]. Also, fattening rabbits housed on straw bedding (which is soiled more readily than flooring without bedding) showed an increased mortality [76]. The prevalence of such health problems is a physiological indicator that maintaining a clean environment for domestic rabbits (i.e. decrease the likelihood of present pathogens) will improve their welfare. Additionally, the cleanliness of captive environments will also improve the welfare of rabbits by increasing their comfort and allowing for a more natural behavioral pattern. Different studies have shown that domestic rabbits prefer to be housed on clean flooring. For example, fattening rabbits would not use soiled flooring [108] and prefer to be housed in cages without straw bedding [107,111–113], only spending time on the straw when it was still fresh and clean [111]. Being able to keep clean is likely an important behavioral pattern for domestic rabbits, as wild rabbits perform grooming behaviors whenever their fur is soiled [27]. Housing domestic rabbits in soiled cages will therefore limit their freedom to respond to discomfort.

Housing conditions. Different aspects of the captive housing conditions of domestic rabbits have been studied as possible welfare threats for most categories of rabbits discussed in this review. This makes sense, as captive housing is a known source of stress for many different species of animals [2,3]. As so much effort has gone into producing scientific knowledge of the effects of housing conditions on the different categories of domestic rabbits, a fairly complete overview can be provided of how to ensure housing conditions do not unnecessarily decrease domestic rabbit welfare. First of all, it can be concluded that domestic rabbits require sufficient space to be able to comfortably perform their natural range of postures and forms of locomotion. In fattening rabbits, breeding does, laboratory rabbits and pet rabbits, an increased range of postures and activities such as hopping and 'playful' jumping are displayed when available space is increased [77,84,87,171,188–190,222]. A study with pet

rabbits showed that domestic rabbits have a preference for a larger cage size and are willing to work for access to it [222]. Increasing the available space per rabbit by decreasing stocking density has also led to better welfare as measured by physiological parameters of health such as mortality and bone quality in fattening rabbits [69–71]. The effect of space availability on stress has also been studied. For breeding does, increased space led to a decrease of stress as measured by fecal corticosterone concentrations [172]. A similar finding was reported for laboratory rabbits, whose performance of abnormal behaviors decreased when they had more space available to them [191]. Additionally, plasma glucocorticoid levels decreased for group housed laboratory rabbits when housed at a lower stocking density [200].

Next, it is recommended for female rabbits to always be housed in groups. In the wild, female rabbits spend their entire life being part of a social hierarchy [28]. Therefore, individual housing will make it impossible for female domestic rabbits to display a full natural behavioral repertoire, as it cancels out any possibilities for social interactions. Studies with female laboratory rabbits have shown that rabbits will actively choose to be in the company of conspecifics [187,192]. It is important to note that a rabbit's natural behavioral repertoire contains both positive and negative social interactions. In order to establish a stable dominance hierarchy, some agonistic interactions are unavoidable. These will determine dominant and submissive positions within the hierarchy, thereby avoiding any further (and more extensive) negative interactions. According to the definition of good animal welfare used in this review, there will only be a decrease in welfare if domestic rabbits cannot adequately respond to such negative social interactions [15]. This can be done by displaying submissive behaviors or by avoiding an aggressive group member. Studies with breeding does and female laboratory rabbits have shown that housing female domestic rabbits in groups without high levels of aggressive interactions is possible [171,196]. Furthermore, decreases in the performance of abnormal behaviors when housed socially have been reported for both categories of rabbits as well [171,177,178,187,190,191,193]. For breeding does, there are many reports of enduring problems with aggression amongst group housed rabbits [163,177–179] . This apparent continued social stress is likely due to the frequent regrouping of individuals that is specific for this category of domestic rabbits [179,180]. However, numerous studies have investigated possible means of allowing successful group housing [177,180,181]. Findings suggest that when does are regrouped in a familiar environment with mostly familiar group members, breeding does will be able to form and maintain a stable dominance hierarchy. More long-term studies to validate these results would be a valuable addition to current knowledge of improving domestic rabbit welfare by housing them in groups.

As mentioned, housing domestic rabbits on straw bedding is not recommended as a measure to improve their welfare. However, the floor type on which rabbits are housed without bedding has also been found to influence their welfare. When given the choice, fattening rabbits and breeding rabbits will avoid contact with floors made of metal wires [88,92,107–109,109,166]. The main difference between a wire net floor and its more preferred alternatives seems to be the abrasive effect of the floor surface actually supporting the rabbits' weight. Metal wire floors are a cause of foot injuries in breeding rabbits [156,173–176]. When given an opportunity to avoid contact with the metal wiring, their foot injuries decrease in prevalence and severity. Therefore, using metal wire floors in rabbit cages is an obvious source of discomfort and possible injury which the rabbits cannot adequately respond to, as contact with the cage floor cannot be avoided. Providing a foot mat will allow for comfortable resting and sitting on a more suitable surface, but comfortable locomotion is only possible when the entire cage floor is made of a more appropriate material such as plastic.

A final conclusion about the effect of housing conditions on domestic rabbit welfare concerns the presence or absence of enrichment. Several different types of enrichment have been shown to be beneficial additions to a domestic rabbit's environment. A platform structure can enhance a rabbit's welfare in numerous ways. First, it increases the available floor space, which has already been discussed as an effective way of improving rabbit welfare. Second, a platform structure can serve the purpose of hiding place within a cage. In the wild, a rabbit's response to a fear-inducing stimulus is to bolt back to its burrow [27,28]. A platform structure can be a simple means of simulating access to a safe place for hiding and resting. This recommendation is supported by studies which have found fattening, breeding and laboratory rabbits will readily use a platform when it is provided to them [78,95,114,126,166,189,192]. Also, the presence of a platform appears to reduce stress. Fattening rabbits housed with a platform inside their cage showed lower levels of fecal glucocorticoid metabolites and fluctuating asymmetry [40,75]. For breeding does, a platform is used as a way to avoid social stress caused by either their kits or other adult females [166,178,184]. Together, these results suggest that a platform structure allows domestic rabbits to have more control over their captive environment and will increase their welfare. Another recommended form of enrichment are food-related items. These will allow rabbits to perform more natural behavior patterns, by simulating foraging behaviors [28]. In laboratory rabbits, it has been found that they prefer food items such as grass cubes or plastic bottles filled with hay to other types of toys [203,204]. These and other studies have also concluded that laboratory rabbits will readily interact with food enrichment, thereby reducing the performance of abnormal behaviors [202,203,205]. Perhaps the success of such degradable enrichment items could be taken as a suggestion that the success of gnawing sticks, a very common means of enrichment for different categories of domestic rabbits, depends on the ease with which they can be destroyed by the rabbits. Although there are many studies reporting successful application of gnawing sticks with fattening and breeding rabbits as measured by their interaction with them [42,86,92,115,116,119–122], there are also reports of fattening and laboratory rabbits lacking interest in them [119,203]. Therefore, using food items as enrichment is likely to be a more successful improvement of domestic rabbit welfare.

Handling. Another common feature in the lives of all different categories of domestic rabbits is regular contact with humans. Being a prey animal, getting picked up and handled by humans is likely a source of fear for domestic rabbits [27,28]. However, studies with domestic rabbits of different ages have shown that they will readily habituate to contact with humans [127,128,130,131,133,209,210]. Therefore, taking the time to accustom domestic rabbits to handling allows them to successfully cope with this aspect of captive life and is recommended as a welfare improvement.

4.2 Suggestions for future research

The overview of domestic rabbit welfare studies provided by this review has also allowed for the determination of possible welfare problems which have not yet received (sufficient) scientific attention. Therefore, no clear suggestions for welfare improvement can be given for these possible welfare problems. It is deemed necessary for the following topics to be the subject of future welfare studies.

Competition over limited resources. As discussed, group housing of (female) domestic rabbits has received much scientific attention. Long lasting agonistic interactions between group members are cited as the main reasons why group housing may be unsuccessful [163,177–179,187]. Such negative social interactions are to be expected from rabbits, as they naturally live in groups by establishing

dominance hierarchies [28,238]. A possible cause for continued performance of aggressive behaviors (and resulting submissive/avoidance behaviors) is competition over limited resources. For example, it has been hypothesized that in wild rabbit groups, competition over food sources would lead to dominant animals foraging in food sites closest to the burrow while those with lower ranks will have to avoid agonistic contact by using food sites farther away (and therefore less safe and less popular)[238]. Interestingly, the concept of competition over limited resources in domestic rabbits reared in captivity has received only limited scientific attention. When group housed, domestic rabbits have access to a limited number of feeders, water bottles and enrichment items. It seems plausible that this could be a source of social tension. Only a single study was found mentioning the possibility of competition over feeders. To measure competition over access to food, feeding time was measured for both dominant and subordinate laboratory rabbits housed in pairs [187]. It was found that feeding times did not differ for rabbits of different ranks. However, the results of this study may not be applicable to domestic rabbits housed in larger groups. Additionally, enrichment items may also be a cause for competition. It would be valuable to know whether the welfare of group housed domestic rabbits can be improved by providing additional feeders or enrichment items to avoid competition. This could enable rabbits to respond to their group members in a better way, as they can then avoid aggression without having to lose access to desired elements in their environment.

Housing conditions adult male rabbits. Adult male rabbits are often housed individually. In the wild, male rabbits live in a group with other male and female rabbits. The males within a group maintain a linear dominance hierarchy by engaging in agonistic interactions [28]. Some males do not join a group but lead solitary lives. Therefore, individual housing seems to be a more severe welfare problem for female rabbits, who are not known to live outside of a social group. Nonetheless, it has been shown that male rabbits' welfare could be affected by individual housing. When housed in standard laboratory cages, male rabbits are inactive for long periods of time and display abnormal behaviors [188]. These indicators of boredom could have been caused by lack of social contact, lack of enrichment or both. Only one study was found which compared the welfare of individually housed to socially housed juvenile male rabbits [197]. This study showed that when bucks are housed in an unstable social environment (where they are regularly introduced to unfamiliar male conspecifics), they show high frequencies of agonistic interactions and appear to be experiencing chronic stress as measured by plasma cortisol level. These indications of poor welfare were not found for bucks housed with a male littermate, nor for individually housed animals. Therefore, stable social housing seems to provide better welfare, as it decreases stress and simultaneously allows for the performance of social behaviors. However, it is possible that bucks will increase agonistic interactions as they become sexually mature. Social housing of adult males has not yet been sufficiently studied. This lack of scientific interest in social housing of male rabbits could be caused by an inability of group housing male rabbits for certain categories of domestic rabbits. Bucks cannot be housed with female rabbits when breeding has to be controlled, as is the case for breeding rabbits. Additionally, when housing several adult male rabbits together, welfare has not always been found to be positive. All-male groups of rabbits show higher levels of aggression [99]. Male rabbits are also more strongly affected by an increase in stocking density as measured by glucocorticoid levels [200]. It would be interesting to see whether restricted social contact could have a positive effect on the welfare of individually housed male rabbits. Enrichment with mirrors to simulate the presence of a conspecific was not successful for male laboratory rabbits, possibly because they could not adequately respond

to the close "presence" of a male of similar size and strength. Perhaps allowing adult males visual contact with other rabbits could decrease any possible stress experienced due to individual housing. This could allow for a more natural behavioral pattern, as interaction with another rabbit is likely more stimulating than interacting with a mirror. Although castration has been suggested as a means for successful social housing of adult males [198,199], this measure is impossible for male rabbits which are used for breeding purposes. For adult males which do not have to reproduce, castration could be a suitable solution, as it would allow for these males to be housed with females. This would be most comparable to rabbits' natural social life .

Cage height. Although several studies have been aimed at the influence of cage height on the welfare of domestic rabbits, all of these studies have used behavioral welfare indicators [105,166]. Their results are not conclusive. Based on these studies, it can be concluded that the rearing up posture is not often used by rabbits living in captivity. This could be explained by the fact that predator avoidance is no longer necessary in captive conditions. However, domestic rabbits have been shown to prefer an increase in cage height during their active period and a decrease in cage height during their resting period. Perhaps domestic rabbits have this preference because being able to rear up and scan their environment (particularly when there is a disturbance) is an adequate response to a stressor. This information is not sufficient as a basis for a welfare recommendation. Firstly, it would have to be established whether standard cage heights are a welfare problem, by adding measurements from physiological indicators of welfare. Similarly, to determine whether an increase in cage height is truly an improvement, a study showing a physiological decrease in stress when rearing up is possible would be valuable.

Welfare Angora rabbits. Only a single study aimed at the welfare of Angora rabbits used for wool production has been found. This study investigated the potential heat loss Angora rabbits experience after their hairs have been collected. However, several other possible welfare problems have been identified for Angora rabbits. These cannot be validated or improved without scientific knowledge of their current welfare status. Although several recommendations can be made based on studies performed with other categories of domestic rabbits, certain elements of an Angora rabbit's husbandry are unique. Mainly, the collection of wool has been suggested as a possible welfare problem. Different methods of wool collection could require different durations of handling/restraint or differences in the level of discomfort and/or pain they cause. Therefore, studies comparing the different methods of collection in terms of their effects on rabbit welfare are recommended as future research.

Welfare ornamental rabbits. Welfare studies have only been found for two of the four types of breeds which have been suggested to experience lowered welfare due to their genotype. Although some scientific attention has been paid to spotted and Angora breeds, it has been very limited in scope. No studies have been dedicated to the welfare status of dwarf and lop-eared rabbit breeds. As possible welfare problems have been suggested for all of these popular types of breeds [229], scientific attention for these problems and suggestions for their improvement are deemed necessary. It is likely that changes in husbandry alone are not going to be sufficient to provide certain breeds of ornamental rabbits with good welfare. For example, if a particular feature is accompanied by disease (as is the case for spotted breeds[230,233]), a change in the breed's standard may be necessary to ensure the welfare of ornamental rabbits is safeguarded. Validation of the

correlation between genotype and resulting welfare problems would be valuable as a basis for such recommendations.

Use of welfare indicators. Most of the welfare studies discussed as part of this review have used welfare indicators which can be used to measure the presence or absence of negative affective states. A lot of the recommendations made are aimed at a decrease of pain, disease and/or stress, thereby increasing positive welfare of domestic rabbits. However, rabbit welfare could also be improved by increasing the occurrence of positive affective states, as stated by the fifth freedom of good animal welfare [15]. A sole focus on suffering makes sense, as the presence of a negative affective state (such as fear or boredom) automatically implies a rabbit is in a state of poor welfare. However, an absence of suffering does not necessarily imply a state of good welfare [19]. This is where welfare indicators of positive affective states could be very valuable. However, only a few studies of domestic rabbit welfare have used indicators of positive affective states. These studies have used an increase in behaviors indicative of a positive affective state as a basis for their recommendations for welfare improvement [e.g. 'playful' forms of locomotion [87,194] and positive social interactions [100,194,197]]. Indeed, play behavior and affiliative interactions have been suggested as the most promising indicators of positive affective states [19,36]. A validation and use of such welfare indicators could be interesting when, for example, a change in housing conditions does not lead to a change in indicators of stress. It is possible that even though neither option causes stress, there could be a difference in welfare as expressed by indicators of a positive affective state.

4.3 Conclusion

Scientific research into domestic rabbit welfare has proven to be very useful, as it provides a basis for recommendations for welfare improvement. These recommendations remain necessary, as common circumstances for the main categories of domestic rabbits are sources of numerous possible welfare problems. By combining the knowledge gathered by different welfare studies, these welfare recommendations can be based on a more complete assessment of domestic rabbit welfare. Based on this review, there are many welfare studies whose results and conclusions are applicable to multiple categories of domestic rabbits. For some welfare problems, these studies have lead to a fairly complete overview. The effects of a domestic rabbit's physical environment on its welfare status are now well understood, as causes for welfare problems such as stocking density and lack of enrichment have received the most scientific attention. Therefore, a suitable physical environment for domestic rabbits can now be provided based on the welfare studies discussed in this review. On the other hand, several gaps in the knowledge of domestic rabbit welfare have also been identified. These are mostly relevant for only a single category of domestic rabbits, possibly explaining why such problems have remained un(der)investigated. How to provide adult (male) domestic rabbits with a suitable social environment remains challenging based on the welfare studies produced so far. Also, Angora rabbits and ornamental rabbits experience specific possible welfare problems which have not yet received scientific attention. As many potential welfare problems have been studied sufficiently for the determination of welfare recommendations, future domestic rabbit welfare research can be aimed at those potential problems that remain mostly untouched by the scientific community.

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Figure 2A: http://www.windward.org/notes/notes67/walt6711.htm
Figure 2B: The impact of the current housing and husbandry systems on the health and welfare of farmed domestic rabbits. *EFSA J.* 267**,** 1–31 (2005) - Picture 5.4
Figure 2C: http://www.arzone.ning.com/profiles/blogs/rabbit-fur

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Figure 3C: The impact of the current housing and husbandry systems on the health and welfare of farmed domestic rabbits. *EFSA J.* 267**,** 1–31 (2005) - Picture 5.5
Figure 3D: http://www.mybunnyfarm.com/bucks/

Figure 4A: Edgar, J. L. & Seaman, S. C. The effect of mirrors on the behaviour of singly housed male and female laboratory rabbits. *Anim. Welf.* 19**,** 461–471 (2010) - Figure 1
Figure 4B: http://www.ahwla.org.uk/site/tutorials/BVA/BVA08-Rabbit/Rabbit.html
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Figure 6A: -
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Acknowledgments

I would like to thank my supervisor Hein van Lith for his advice and support all throughout the process of writing this review. I have enjoyed immersing myself in the subject of rabbit welfare and have come away from this project with a greater knowledge of welfare research in general. This project has been a valuable addition to my master's programme. Also, I would like to thank Frauke Ohl and the department of Animals in Science and Society for making me feel like part of the team. It has been a pleasure to work in your company.

Layman's summary

In this review, the different welfare problems faced by domestic rabbits are discussed. Rabbits are housed in captivity for various different reasons. The main categories of domestic rabbits are fattening rabbits (kept to produce meat), breeding rabbits, laboratory rabbits, pet rabbits, Angora rabbits (kept to produce wool) and ornamental rabbits (so-called fancy breeds which are presented in rabbit shows). In the wild, rabbits are social animals which usually spend most of their time foraging for food. This cannot always be replicated in captivity. As a result, all of the categories of domestic rabbits face possible welfare problems. Some of these are common to all or most categories of rabbits, such as welfare problems caused by small cages or keeping rabbits in social isolation. Others are specific to a certain category, such as the slaughtering of fattening rabbits or the plucking of wool from Angora rabbits. Welfare research is a valuable source of information on which suggestions for welfare improvement can be based. However, studies of rabbit welfare have so far been aimed at only a single category (e.g. studied the effects of cage size on laboratory rabbits). In this review, the knowledge gathered by welfare studies for all different categories is combined. This produces a more complete overview of the effects of different welfare problems. Also, it shows which possible welfare problems have not yet received sufficient scientific attention. It was found that effects from the physical environment of domestic rabbits (containing aspects such as cage size, floor type and enrichment items) have been studied extensively. This research effort has produced suggestions for better welfare, such as increasing cage size and providing suitable enrichment items. Problems related to improper feeding and handling by humans have also received sufficient attention to produce recommendations for welfare improvement. Therefore, it is suggested that future domestic rabbit welfare studies are aimed at possible welfare problems which have not yet received sufficient attention. The welfare effects of adult rabbit's social environment are not yet fully understood. The social demands of adult males in particular require further study. While female rabbits clearly benefit from being housed with other rabbits, further studies aimed at reducing possible aggression amongst them are deemed necessary. Finally, the category-specific possible welfare problems faced by Angora rabbits and ornamental rabbits have hardly received any scientific attention. It is suggested that future studies will investigate whether their welfare is in fact threatened by current common practices. If so, suggestions for welfare improvement will also be required for these categories of rabbits.