FINAL REVISION
Accepted for publication in Animal Welfare

Do rabbits need each other? Effects of single versus paired housing on rabbit body temperature and behaviour in a UK shelter

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Running title: Do rabbits need each other?

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Abstract

In the wild, rabbits are social but territorial. Recent surveys suggest that over half of pet rabbits are housed singly. We aimed to compare welfare in single versus paired rabbits. We predicted singletons would show more abnormal or escape behaviour, greater stress responses to handling, and reduced body temperature (being unable to huddle with another individual when cold), but that pairs may show aggression. This study was conducted during wintertime at a rabbit-only rescue centre, and included 45 rabbits, comprising 15 housed singly and 15 pairs. Like most pet rabbits, they were housed either outdoors or in unheated outbuildings. Singletons were mostly in smaller enclosures than pairs. Home-pen observations (40 min) revealed bar-biting in 8/15 single rabbits compared with 0/30 of the paired ones ($p < 0.001$). No other behavioural effects of social housing reached significance, and enclosure size showed no significant effects. Body temperature was significantly lower in singletons than pairs (aural: $p = 0.042$; rectal [significant in outbuilding-housed rabbits only]: $p = 0.026$), with at least 0.5ºC mean difference. On colder days, rabbits adopted compact postures more ($p = 0.049$), and relaxed postures less frequently ($p = 0.046$). After handling, pairs resumed normal behaviour significantly more quickly than singletons in the home-pen (3.0 +/- 0.3s versus 8.3 +/-1.3s, respectively). Aggression was never observed. The results indicate that social housing reduces bar-biting, aids thermoregulation, and may help buffer stress. Rabbit owners should be encouraged to meet the need for rabbits to be housed with an appropriate conspecific in a suitably large, sheltered enclosure.

Keywords: Abnormal behaviour; Animal welfare; Rabbits; Social buffering; Thermoregulation

Introduction

In the wild, rabbits are a social species, but surveys indicate that between 54% (PDSA 2018) and 58% (Rooney *et al.* 2014) of UK pet rabbits are kept singly, and single housing is also common in rabbits kept by UK breeders (Gosling *et al.* 2018). Approximately 63% of pet rabbits are kept singly in Australia (Howell *et al.* 2015), and around 50% in the Netherlands (Schepers *et al.* 2009) and the US

and Canada (Welch *et al.* 2017). This is potentially a violation of one of the Five Needs outlined in the UK Animal Welfare Act 2006: that 'animals should be housed with, or apart, from other animals as appropriate for the individual and species' (Parliament of the United Kingdom 2006). In a survey of people buying rabbits in the UK, 60% believed that human company could suffice instead of a second rabbit, and 40% were planning to keep their new rabbit alone (Edgar & Mullan 2011). In a Delphi consultation involving 11 rabbit welfare experts (7 continuing to completion), inappropriate social grouping was recognised as being a severe and lasting welfare issue, but it was not selected as a key priority issue for rabbit welfare (Rioja-Lang *et al.* 2019). There are arguments both for and against social housing of rabbits.

Potential reasons for solitary housing of rabbits

Whilst a social species, wild rabbits are territorial, occupying individual burrows within a larger warren where the habitat allows, and defending them from intruders (Cowan 1987a; Cowan 1987b). Aggression in captive rabbits constitutes a welfare concern for the victim who cannot escape, as well as possibly for the aggressor, depending on the reasons for aggression. Rabbits can be difficult to pair successfully because of aggressive behaviour (Crowell-Davis 2007). Approximately 48 of 52 pet rabbits housed with at least one other rabbit in a UK survey showed some antagonistic behaviour (chasing and mounting), but only four had ever been injured by their companion, and all owners reported their rabbits' relationships as 'friendly', rather than aggressive (Mullan & Main 2006). In another survey of over 1000 rabbit owners, approximately one quarter of rabbits were reported to at least occasionally show aggression, competition and/or avoidance towards each other (Rooney *et al.* 2014), so it is conceivable that in some cases, social housing could negatively affect rabbits. In a study of rabbit preference, both dominant and subordinate laboratory rabbits showed a preference to be apart from their pen-mates, but only if the solitary pen was of equal size and quality to the group pen; if it was small and barren, they preferred to be in the home-pen with their group (Held *et al.* 1995).

Owners' reasons for solitary housing may include financial and space limitations (Edgar & Mullan 2011), concern that rabbits might fight (Crowell-Davis 2007), and possibly a sense of it being 'normal' to own 'a rabbit' (e.g. the current authors' google search on 9th January 2020 for "getting a pet rabbit" returned 151,000 hits, whilst "getting pet rabbits" returned 906 hits). Importantly, rabbits may also be kept singly to avoid unintended breeding if there is a risk that entire rabbits of the opposite sex are housed together (e.g. through lack of confidence in rabbits being accurately sexed (Antinoff 1999), reluctance to neuter rabbits (Edgar & Mullan 2011), or at breeding establishments (Gosling *et al.* 2018)). Unplanned breeding and thus having too many rabbits is the most common reason declared for rabbit relinquishments in the UK (Ellis *et al.* 2017). There may, however, be negative welfare consequences to solitary housing.

Potential reasons for social housing of rabbits

Tests of motivation, in which rabbits were required to push through weighted doors to access different resources, showed that rabbits seek social contact almost as much as food, and more than the other resources tested (a raised platform or extra space (Seaman *et al.* 2008)) (but see Held *et al.* 1995). This motivation for companionship may be partly due to perceived security when with a conspecific, via a phenomenon known as 'social buffering'. Consistent with this, lone pet rabbits behaved more fearfully than socially housed ones in an open field test (Schepers *et al.* 2009). In other social species, social housing also decreased stress responses to challenges (e.g. in calves (De Paula Vieira *et al.* 2010) and rats (Sharp *et al.* 2002)). Social housing even improved wound-healing rates compared with rates in singly housed animals (e.g. in mice: Van Loo *et al.* 2007).

Single housing may increase the risk of abnormal or escape-related behaviour. In laboratory rabbits, singletons in standard cages showed significantly more bar-biting and digging behaviour compared with paired ones in larger cages or pens (Podberscek *et al.* 1991; Chu *et al.* 2004). Single housing also decreased activity levels and increased rates of abnormal and escape-related behaviour in rats (Hurst *et al.* 1997, 1998). It is thus possible that single housing may decrease activity and increase abnormal or escape behaviour in companion or shelter rabbits, similarly.

Social housing may also enable thermoregulation via huddling when ambient temperatures are low or conditions are damp. Body temperature was significantly higher in socially than singly housed hamsters (Kauffman *et al.* 2003) and – at night only – mice (Van Loo *et al.* 2007). This could be important for pet rabbits in the UK (where temperatures average around 5ºC during winter and regularly drop below freezing at night), because over 71% of such rabbits are reported to live outdoors or in unheated sheds or out-houses (Rooney *et al.* 2014).

Study hypotheses

We thus predict that compared with single rabbits, pair housed ones will:

- be more active and perform less abnormal or escape behaviour in the homecage;

- have warmer body temperatures and, correspondingly less compact, heat-conserving postures; and

- have lower heart rates and settle more quickly after handling and temperature measurement;

- but may show occasional aggression.

The study was carried out at a rescue shelter housing only rabbits, which could hold up to 200 rabbits at the time. The work was designed with the agreement and advice of the shelter's Founder and Manager.

Methods

Animals and Husbandry

The study comprised 15 single rabbits and 15 pairs of rabbits (45 rabbits in total). Rabbits received feed pellets (Burgess^{TM}) and fresh vegetables daily, water and hay ad libitum, and were provided with environmental enrichment (tunnels, artificial warrens and chew toys). Paired rabbits were housed outdoors in large 1.83 x 0.91 m hutches or walk-in aviaries up to 3.05 x 2.44 m, while single rabbits were in large indoor or outdoor hutches (1.52 x 0.61, 1.83 x 0.61, or 1.22 x 1.22 m), or pens up to 1.83 x 1.22 m. All enclosures had bars that could be bitten, with more bars in larger enclosures generally, although the precise area of bars per enclosure was not quantified. No rabbits were singly

housed for the purposes of the study. Instead some of the rabbits had arrived singly at the Rescue, or their partner had died, and, after a few weeks of acclimatisation (and after recovery from neutering if necessary), attempts were made to bond them with a compatible partner according to the normal procedures at the Rescue (Enright Unpublished 2015). Bonding was usually successful, but with some individuals it could take many weeks to find the right partner if any could be found. Most socially housed rabbits comprised neutered female-male pairs, but occasionally they comprised rabbits of the same sex (e.g. siblings). No bonding sessions were delayed for the sake of the study.

For inclusion in the study, rabbits had to have been present at the Rescue for at least 2 weeks before observations began, and all the pairs established for at least 3 weeks. The Rescue Manager advised as to which rabbits would be suitable for inclusion in the study on the basis of health and handleability. Only healthy rabbits accustomed to handling were used. Rabbits who were currently unwell, or were likely to be particularly fearful or aggressive during handling were excluded. We did not restrict the rescue manager's selection in terms of breeds, ages, and sexes.

The rabbits were habituated to the presence of the observer (PS) during twice-weekly pilot observations over a period of up to 6 weeks, and the observer also assisted with rabbit husbandry during that time.

The project received ethical approval from the Clinical Research Ethical Review Board at the Royal Veterinary College (URN 2015 1372).

Behavioural observations in the home-pen

Each rabbit/pair was observed for two 20 min periods between 10:00 and 16:00 on the same day during January and February 2015. The two observations were separated by approximately 2.5h (mean+/-SE=156.4+/-9.4 min), and were timed to avoid mealtimes and husbandry activities. The observer (PS) stood 0.6-0.9 m from the front of the rabbits' enclosures and recorded behaviours defined using an ethogram devised during pilot observations (Table 1).

<Table 1 about here>

Every 2 min during each observation period, defined states such as posture and location were recorded instantaneously, while the frequencies of more fleeting event behaviours such as bar-biting or grooming were recorded using one-zero sampling during the intervening 2 min periods (Martin & Bateson 2007). For pairs, scan sampling was used to equitably record the behaviour of both rabbits within each 20 min period (there was no need for this for singletons, as only one rabbit was present). Due to resource constraints, unfortunately it was not possible to systematically video the behaviour for subsequent blind inter-observer reliability testing. The observer was aware of the risk of unconscious bias, and – before observations began – we explicitly discussed the responsibility of an observer to be open to whatever the data reveal about animal needs. For example, we acknowledged that evidence was currently quite contradictory about whether rabbits should or should not be socially housed.

Handling and physiological measurements

To test the social buffering hypothesis, we monitored the response of the rabbits to gentle handling on a table to take their body temperature. This was carried out after the home-pen observations and on a different day. All the rabbits in the study were used to being handled, so relatively little stress was anticipated, but the precise handling experience used here was unusual for the rabbits. Handling was carried out by PS and an assistant, with the advice and close supervision of the highly experienced Rescue Manager. The rabbits were monitored closely for signs of stress (e.g. proactive responses such as struggling or avoidance, and reactive responses such as tension or 'freezing'). If these signs were observed in a rabbit, it was immediately returned to its carrier and given a treat before being returned to the home-pen.

We used an in-ear thermometer (Braun ThermoScan® ExacTemp Ear Thermometer) to take rabbit temperatures. However, during pilot studies we discovered that readings were only realistic for lop-eared rabbits; for rabbits with wild-type ears, the readings were often implausibly low because most rabbits were kept outdoors and their ears were exposed to external temperatures. This created many missing values. We continued to use the ear thermometer, but also used a digital plastic rectal

thermometer (Brannan™) that was used at the Rescue centre and was reported by the staff to be generally well-tolerated by the rabbits. To record rectal temperature, a rabbit was placed on the table, and a lubricant gel (KY jelly) was applied to the anus; one arm was lightly curved around the rabbit for security and to discourage movement, but not to prevent it. The thermometer was then gently inserted into the anus to 1.5 cm depth, the minimum depth to ensure the bulb was no longer exposed. The thermometer was sterilised using Milton™ fluid between rabbits. At no point was any rabbit turned onto its back, as is recommended in some veterinary texts, as this would have caused tonic immobility (Oxley *et al.* 2018). If any rabbit showed persistent signs of resistance or relatively intense stress, the process would be stopped immediately. For paired rabbits, their pen mate was close by and within view, inside the carrier used to transport the rabbits from their pens to the table.

After the ear and rectal temperature readings were taken, the rabbits' heart rates were monitored using a paediatric stethoscope (Littmann® 3100 Electronic Stethoscope). To do this, the rabbits' forelimbs were lifted slightly and the stethoscope applied to the chest for 20-30s. The entire handling process lasted 5-10 min per rabbit.

Time to settle was recorded as the latency between being placed back into their home-pen and starting to resume normal behaviour: to eat, drink, groom or re-emerge from their shelter if they had entered it.

Statistical analysis

For homecage behaviour, data were summarised as the total number of timepoints in which each behaviour was observed (max. = 20 for a behaviour observed at every 2 min interval over the full 40 min). To control for there being two rabbits per pair and enable contribution of data from all rabbits to the final dataset, values were averaged for pairs.

Data were analysed using SPSS (version 24, IBM™). For behaviour and other measured responses that generated normally distributed model residuals, General Linear Models were used. Some single rabbits were housed in enclosures within a barn, so to account for the partial overlap of single housing

with indoor housing, three housing treatments were compared: Paired, Single outdoors, and Single indoors. This variable was used as a predictor when possible. For variables with too many missing values, this was not possible, so separate models testing social condition and then enclosure location were run instead. Other predictors tested as covariates alongside the housing treatment(s) were age, days spent at the shelter, rabbit size, and enclosure space per rabbit. Some of the predictors correlated (e.g. younger rabbits tended to have been at the shelter for less long than older rabbits), so if a model could not support both together, separate models were run, first with one of the predictors and then with the other. Breed was too diverse to be meaningfully included, and sex could not be included because pairs mostly comprised one rabbit of each sex. The residuals were checked for normality and responses were transformed using square root or log functions if necessary.

For responses relevant to thermoregulation (body temperature, compact/relaxed posture and huddling), the average environmental temperature on the day of the measurement (estimated from http://www.weatheronline.co.uk) was also included as a predictor to account for some days having been colder than others.

For temperature, heart rate and time to settle down after handling, only data from the first rabbit to be handled within a pair was used in the above analysis, because the first rabbit had more of an equivalent experience to the singletons (the second rabbit had to wait in its carrier while the first was handled). Additionally, General Linear Mixed Models were performed to assess whether temperature, heart rate or settling down was affected by the order in which the rabbits were handled (first or second within a pair), alongside the other predictors listed above. There was no significant order effect so, when the ear temperature model initially could not run because there were too many missing values for the first rabbits, the average values for each of the pairs were used instead for that variable.

When data included many zeros, the data were converted to binary form and tested using binary logistic regression, using the same predictors as described above. However, bar-biting showed complete separation of data (the response was entirely absent in paired rabbits), so social condition

had to be excluded from the model, and its effect tested separately using a non-parametric binomial test.

Results

Demographics

Details of the rabbit signalment and housing is shown in Table 2. Just 4/15 singletons were does (females), compared with 14/30 paired rabbits. There was a wide range of sizes and breeds in both groups. Singletons were younger than paired rabbits, with means of approximately 1 year and 10 months versus 3 years and 10 months, respectively, and had been at the rescue for less long. Two of the singletons were single because they had previously been in an agonistic relationship, but all rabbits were successfully paired after the study was completed.

The enclosures were heterogeneous, with many being handmade or donated. Singletons had smaller enclosures than pairs, but there was some overlap in terms of space per rabbit, with singletons in the largest enclosures having more space per rabbit than paired individuals in the smallest social enclosures (Table 2). Most rabbits were housed outdoors, but five singletons were housed in enclosures within a barn.

<Table 2 about here>

Home-pen behaviour

Single rabbits were significantly more likely to show bar-biting behaviour than were paired rabbits; whilst over half the single rabbits showed the behaviour, no paired ones were observed to perform it at all (Singletons bar-biting = 8/15 rabbits; Pairs = 0/15 pairs; $P < 0.001$; Figure 1). Although single rabbits had smaller enclosures than pairs did (Table 2), space per rabbit had no significant effect on bar-biting ($p = 0.488$), and neither did being outdoors versus in the barn ($p = 0.371$).

<Figure 1 about here>

Of the other behaviours that could be performed by rabbits in both housing treatments and were seen frequently enough for statistical analysis, none showed significant differences between singletons and pairs or most other predictors. The behaviours tested were Compact posture, Front of cage, Resting, Digging, Locomotion and Grooming. The only significant effect was that when external temperatures were warmer, rabbits adopted relaxed postures more (coeff+/-s.e = 0.757+/-0.355; $F_{1, 19} = 4.543$; p = 0.046), and compact postures less (coeff+/-s.e = -0.755+/-0.360; $F_{1, 19} = 4.404$; p = 0.049). External temperature did not significantly affect huddling behaviour (P = 0.106) – the mean +/- S.D. air temperature during the behaviour observations was 6.6 +/- 3.5ºC.

Paired rabbits huddled together on 5.3 +/- 1.5 of the 20 time points observed, equating to approximately 26.5% of their time. They were seen performing active social behaviour on 6.2 +/- 1.5 of the time points, equating to approximately 31% of their time. No aggressive behaviour was seen at any point in the study.

Body temperature

Single rabbits were significantly colder than paired ones (Figure 2), both when temperature was measured aurally ($F_{1, 10} = 5.08$; P = 0.042) and rectally ($F_{2, 22} = 4.34$; P = 0.026). For rectal temperature, post-hoc analyses revealed that it was the singletons housed in the barn who were significantly colder than outdoor pairs (coeff+/-s.e. = -0.647+/-0.220; P = 0.007). The effect sizes were fairly large; for example singletons had rectal temperatures on average 0.5ºC colder than pairs (Mean+/-S.E. Paired = 38.3+/-0.1ºC; Single = 37.7+/-0.1ºC). There were no significant effects of age, size, space allowance, time at the rescue, or air temperature on body temperature. The mean +/- S.D. estimated air temperature during the handling session days was 6.2 +/- 1.8ºC.

<Figure 2 about here>

Social buffering

Paired rabbits took significantly less time to settle down and resume normal behaviour after handling than did singletons ($F_{1, 20} = 5.03$; P = 0.036; Figure 3). However, all rabbits resumed normal behaviour within 20s (Pairs mean +/- S.E. = 3.0 +/- 0.3s; Singletons = 8.3 +/-1.3s).

<Figure 3 about here>

Heart rate was not significantly affected by social condition (mean+/-s.e.: Single = 243.5+/-7.8 bpm; Paired = 261.8+/-15.4; P = 0.079; preliminary analysis had suggested a possible effect, but this disappeared once body size could be included in the model (Burn & Shields 2015)). There were no significant effects of the other predictors on heart rate or time to settle.

Discussion

This study aimed to compare the welfare of single versus paired rabbits in terms of home-pen behaviour, thermoregulatory ability, and social buffering during potentially challenging handling. Pair housing decreased the number of rabbits bar-biting, appeared to help them maintain a warm body temperature, and enabled them to resume normal behaviour more quickly after handling. The implications of each of these findings will be discussed in turn.

Home-pen behaviour

Most behaviour was not significantly affected by social condition, but over half of singletons bit the bars of their enclosures, compared with none of the paired rabbits. This is despite there having been twice the number of individual rabbits comprising the pairs here (i.e. 0/30 paired rabbits bar-bit versus 8/15 singletons). This agrees with findings regarding single laboratory rabbits, who performed more bar-biting (and digging) than socially housed ones (Podberscek *et al.* 1991; Chu *et al.* 2004).

The likelihood of bar-biting here was not significantly greater in smaller enclosures, but, because singletons had smaller enclosures than pairs, this remains a potential confound that requires further investigation, as bar-biting might be expected to occur more in smaller enclosures. We were able to

separate the effects to some degree, because space per rabbit could be included within models on a scale, and there was some overlap between paired and single rabbits in available space. In all previous studies comparing social versus individual rabbit housing, the confound between social and spatial housing has existed even more starkly than here, because all singletons were in small cages and all social groups in large cages/pens with no overlap (Podberscek *et al.* 1991; Chu *et al.* 2004). It is thus currently difficult to separate the effects of social condition and space allowance. In studies investigating the effect of cage size on rabbit behaviour, smaller cages significantly reduced activity levels and interaction with the environment, but effects on bar-biting were not reported, and either singletons only (Dixon *et al.* 2010; Bignon *et al.* 2012), or group-housed rabbits only (Buijs *et al.* 2011) were included. One study – on rats – housed animals in different group sizes whilst keeping the cage size constant, and found that singletons showed significantly more escape-related behaviour (including bar-biting) than socially housed rats (Hurst *et al.* 1999). Clearly, the effects of social condition and enclosure size on rabbit behaviour including bar-biting need to be separated in future studies. Nonetheless, in applied contexts owners appear to be more likely to provide larger enclosures if they have more than one rabbit (Rooney *et al.* 2014; Gosling *et al.* 2018), so in practice the two factors may often be interrelated.

Bar-biting is not uncommon in pet rabbits, with one survey finding that 26.6% of pet rabbits in Italy performed stereotypic behaviour, described as including 'bar-gnawing and cage-pacing' (Normando & Gelli 2011). Bar-biting is usually an indicator of negative welfare, although it can have several different causes. In a series of controlled experiments, mice predominantly chewed bars that formed the exit route rather than other available bars, suggesting that the behaviour reflects a motivation to escape (Nevison *et al.* 1999; Lewis & Hurst 2004). If the same is true for rabbits, it could mean that singletons here were more motivated to escape from their pens than pairs were.

A further explanation for bar-biting behaviour is that, if it is very persistent, it can become a stereotypic abnormal behaviour. Bar-biting can be a stereotypy in many species including pigs, rats and bears (Mason & Rushen 2006). In these cases, the behaviour is not only caused by suboptimal

conditions, but can itself cause further welfare compromise including oral lesions, dental damage and – if performed highly perseveratively – animals may fail to perform sufficient maintenance behaviour. It is not known if this occurs to such a pathological extent in rabbits. Nevertheless, whether the bar-biting in singletons is stereotypic or an escape behaviour, or both, the fact that over half the singletons here exhibited the behaviour, compared with none of the paired rabbits, strongly suggests that single housing (especially in smaller enclosures) affects them negatively.

There were no effects of social condition on any other measured home pen behaviour. It is possible that other effects might have been observed with more intensive behavioural observation schedules, including night time observation, especially as we were only able to observe rabbits for 40 min each in total. It is worth noting that, under the observation schedules used here, the main potential negative effect of social housing – aggression – was never observed. This partly confirms observations from another study carried out at the same rescue centre, which investigated dominance and aggression in 24 pairs of rabbits (Enright Unpublished 2015); in those rabbits there was no serious aggression during three 20 min observations per pair and two resource competition tests, although nipping was seen in eight pairs and two pairs showed brief fighting. However, the absence of aggression may conflict with results from surveys regarding pet rabbits, where one quarter (Rooney *et al.* 2014) to three quarters (Mullan & Main 2006) of socially housed rabbits showed occasional agonism. This could be because of the short observation window in the current study, but also because paired pet rabbits may not be typified by these neutered opposite-sex and sibling pairs, who were provided with much environmental enrichment and paired via an iterative matching process (similar to that described by Guard Unpublished). In any case, aggression could negate the otherwise beneficial effects of social housing, so the compatibility of individual rabbits is an important factor to consider.

Thermoregulation

Rabbits were significantly warmer when housed in pairs. The median aural temperature differed by more than 1°C between the two groups, and the rectal temperature by approximately 0.5°C; rectal temperatures are more reliable and less variable than aural ones (Chen & White 2006),

albeit more invasive, but the fact that we have found similar significant effects when using both measurement techniques here consolidates the finding. These measurements are likely to be relatively robust to any unconscious bias from the experimenter, because the thermometers were both digital, giving a final temperature reading only. This effect of social housing on body temperature could be important, because colder rabbits are more susceptible to disease (Small *et al.* 1986) and more likely to die in a clinical context (Di Girolamo *et al.* 2016).

The likely mechanism underlying the temperature difference found here is unknown. It seems unlikely that the paired rabbits were showing stress induced hyperthermia, as observed in socially stressed rabbits in unfamiliar environments (Graf *et al.* 2011), because social stress was not reflected in the behavioural observations, and stress-induced hyperthermia is an acute response, whereas the paired housing was long term. Also, the mean rectal temperatures (Paired = 38.3+/-0.1ºC; Single = 37.7+/-0.1ºC) in the current study were colder – not warmer – than the usual range expected for rabbits, which is usually between 38.5 and 39.9ºC (Lee 1939; Gonzalez *et al.* 1971; Chen & White 2006; Di Girolamo *et al.* 2016). Another reason why paired rabbits were warmer than singletons could be that only paired rabbits were able to huddle together if cold, which pairs were observed to do on over a quarter of observations. However, colder external air temperatures did not significantly increase huddling behaviour. This could mean that rabbits were cold enough to motivate huddling equally at all the (winter) temperatures within the study period, creating a 'ceiling effect' for huddling. Alternatively, if rabbits were not especially cold, it could mean that they huddled for reasons other than thermoregulation, e.g. for affiliative reasons or perceived security. Consistent with the current findings, environmental temperatures between 5 and 23ºC did not significantly affect huddling duration in post-weaned European rabbits kept in a laboratory (Seltmann *et al.* 2009). In fact, rabbits were able to maintain a stable body temperature at ambient temperatures down to 5ºC (Gonzalez *et al.* 1971); temperatures below this appear not to have been tested.

The rectal temperature here only reached significance in singletons when housed in the barn rather than outside, which is perhaps surprising. Staff at the rescue shelter suggested that this could

have been because outdoor rabbits were provided with deeper bedding in anticipation of the cold, and that outdoor shelters may have been more draught-proof than indoor ones, where the barn was expected to provide additional protection from the cold. This study was not designed to compare outdoor versus barn housing, so interpretation of the result is speculative and the finding requires replication.

Because the rectal temperatures in the current study were colder than in other studies (Lee 1939; Gonzalez *et al.* 1971; Chen & White 2006; Di Girolamo *et al.* 2016), it is necessary to consider why this might have occurred. This is most likely to be because we inserted the thermometer less far (1.5 cm) into the rectum than described in most other reports (e.g. 3 cm: Di Girolamo *et al.* 2016) and rectal temperatures increase with depth (Lee, 1939). At a depth of 2.5cm, mean rectal temperatures were approximately 37.5ºC (Lee 1939), similar to values in the current study, although Chen and White (2006) inserted thermometers only to a depth of 1cm and obtained a higher mean temperature of 39.3ºC. Our study was also conducted at colder ambient temperatures than other studies, so it is possible that this was a contributing factor to the low body temperatures.

The question remains as to whether the single rabbits here were cold to the point of discomfort, as we recorded their mean rectal temperature to be 37.7ºC, which is below the 37.9ºC threshold defining hypothermia in rabbits (Di Girolamo *et al.* 2016). We found that rabbits did adopt more compact, and less relaxed, postures during colder weather; those behaviours showed no significant differences between the two social conditions, so rabbits appeared to respond similarly to cold conditions, regardless of social condition.

Pet rabbit care advice sheets suggest that UK pet rabbits ‘cope well’ with cold temperatures and do not usually need to be brought indoors, as long as plenty of bedding and food are provided and the outdoor shelter is protected from draughts and dampness (e.g. RSPCA 2013). However, the fact that the singletons had significantly colder body temperatures is still concerning, especially as most companion rabbits are kept outdoors or in unheated outhouses and some of these may not be protected as advised (Mullan & Main 2006; Rooney *et al.* 2014). Indeed the rectal temperatures recorded here

suggest that, under some circumstances, rabbits might sometimes be colder in an outhouse than outdoors. Cold temperatures were a significant predictor of subadult mortality in wild type European rabbits in a semi-natural enclosure, with around 10-20% dying when the mean temperature was 2°C, and approximately 50% dying when the mean temperature was 1°C (Rödel *et al.* 2004). Leaving rabbits outdoors in such temperatures should thus probably be avoided if possible, unless the enclosure can be properly insulated, and the current results suggest that this may be particularly important for single rabbits. Some organisations have recently advised housing rabbits socially, partly to assist with thermoregulation in cold weather (e.g. Save a Fluff 2018).

Social buffering

Paired rabbits resumed normal behaviour more quickly after handling, which is consistent with the social buffering hypothesis, whereby having their pen mate present either during handling, afterwards, or both may have helped them cope with that potential challenge. The behavioural observations were not conducted blind to the hypothesis, so the results require confirmation through further research. However, the current findings fit with the previously observed increase in open field vigilance in solitary pet rabbits (Schepers *et al.* 2009), and examples of social housing increasing resilience to challenge in other species (Kikusui *et al.* 2006). In the wider context of pet rabbits, this implies that social housing might help reduce stress responses to common challenges such as nail-clipping or veterinary treatments.

The heart rates here (Single = 243.5+/-7.8 bpm; Paired = 261.8+/-15.4) were within the normal reference range of 198 to 330 bpm for rabbits (Lord *et al.* 2010), and we did not find that heart rate was significantly faster during handling of single than paired rabbits. Considering that 61% of pet rabbits were reported by owners to show some signs of stress when handled (Rooney *et al.* 2014), perhaps there was a ceiling effect on heart rate, which could have meant that stress was equally high during handling regardless of social condition.

Conclusion and animal welfare implications

Social housing in this rescue centre population appeared to prevent bar-biting, enable rabbits to maintain warmer body temperatures in wintertime, and lead them to resume normal behaviour more quickly after handling. The results may apply to pet rabbits as well as those in shelters, as this population comprised rabbits originally from the pet population, and the rescue shelter cared for the rabbits in accordance with best practice for outdoor housed pet rabbits. The results suggest that, when possible and when the compatibility of the individual rabbits is not an issue, rabbits should be socially housed to safeguard their health and welfare. It is likely that human company cannot replace a rabbit companion as some owners believe (Edgar & Mullan 2011), because humans cannot help with thermoregulation or provide stimulation and security on a constant basis. For rabbits that have to be singly housed, they should be housed in a warm environment and gradually habituated to handling using positive reinforcement to help provide stimulation and resilience. We suggest that veterinarians, relevant charities and pet shop staff should help convey this message to prospective and current rabbit owners, ensuring that the rabbit's need for companionship of its own kind is properly and responsibly met.

Acknowledgements

Many thanks to Jamie Enright who provided technical assistance and constructive comments in this project. We are grateful to Caroline Collings for her time, expertise and support of the project as well as to Vicki Crisp, Lea Facey and other volunteers and supporters of the Rabbit Residence Rescue, Royston, Hertfordshire. This project was conducted in part fulfilment of Pamela Shield's BSc in Bioveterinary Sciences at the Royal Veterinary College.

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Figures

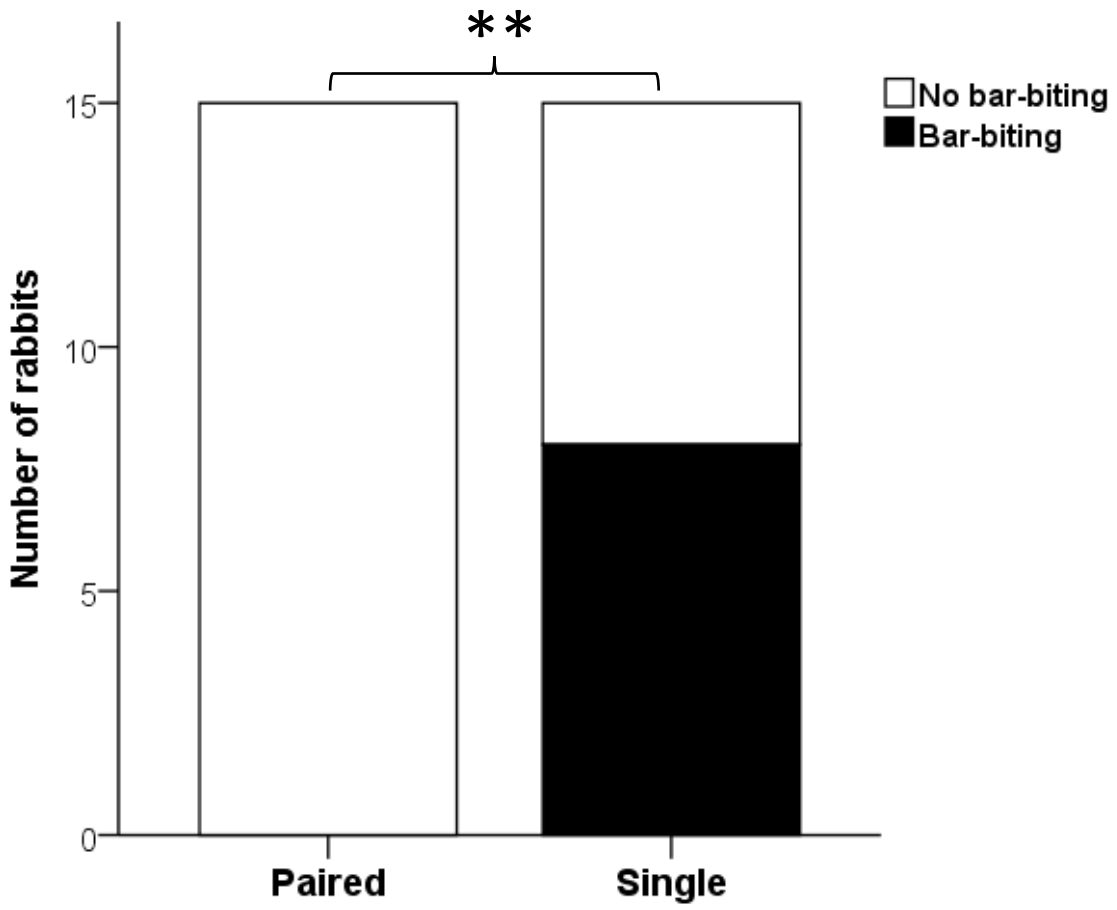

Figure 1. Numbers of rabbits or pairs of rabbits showing bar-biting. Black = Bar-biting was observed; White = bar-biting was not observed. **Single housed rabbits were significantly more likely to show bar-biting than were pairs ($P < 0.001$).

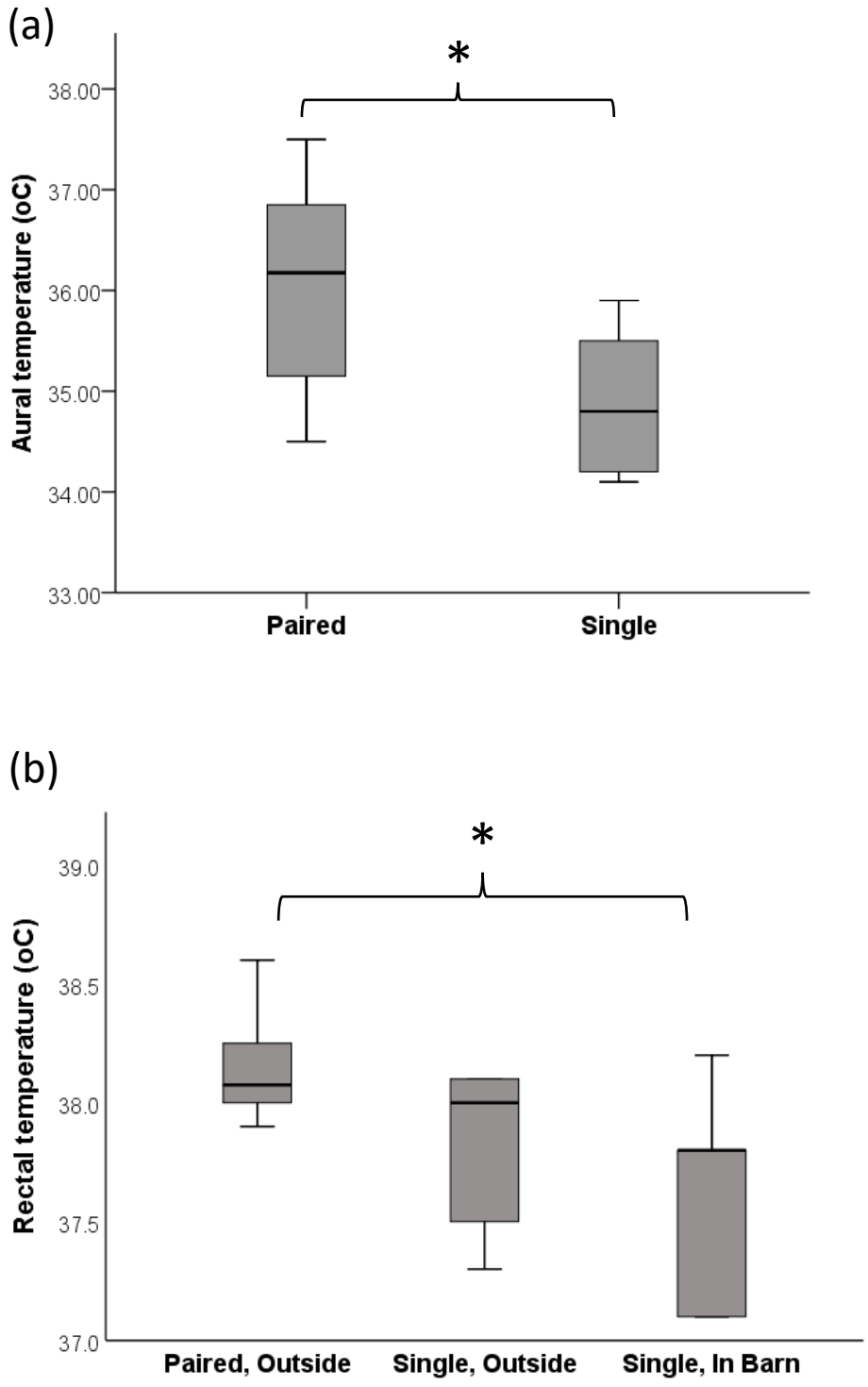

Figure 2. Body temperatures of single and pair housed rabbits. Temperature was digitally recorded both (a) aurally and (b) rectally. Single rabbits were analysed separately according to whether they were housed outside or in a barn where possible, but this could not be done for aural temperature due to missing data (only two of the rabbits in the barn had ear temperature values). *P < 0.05.

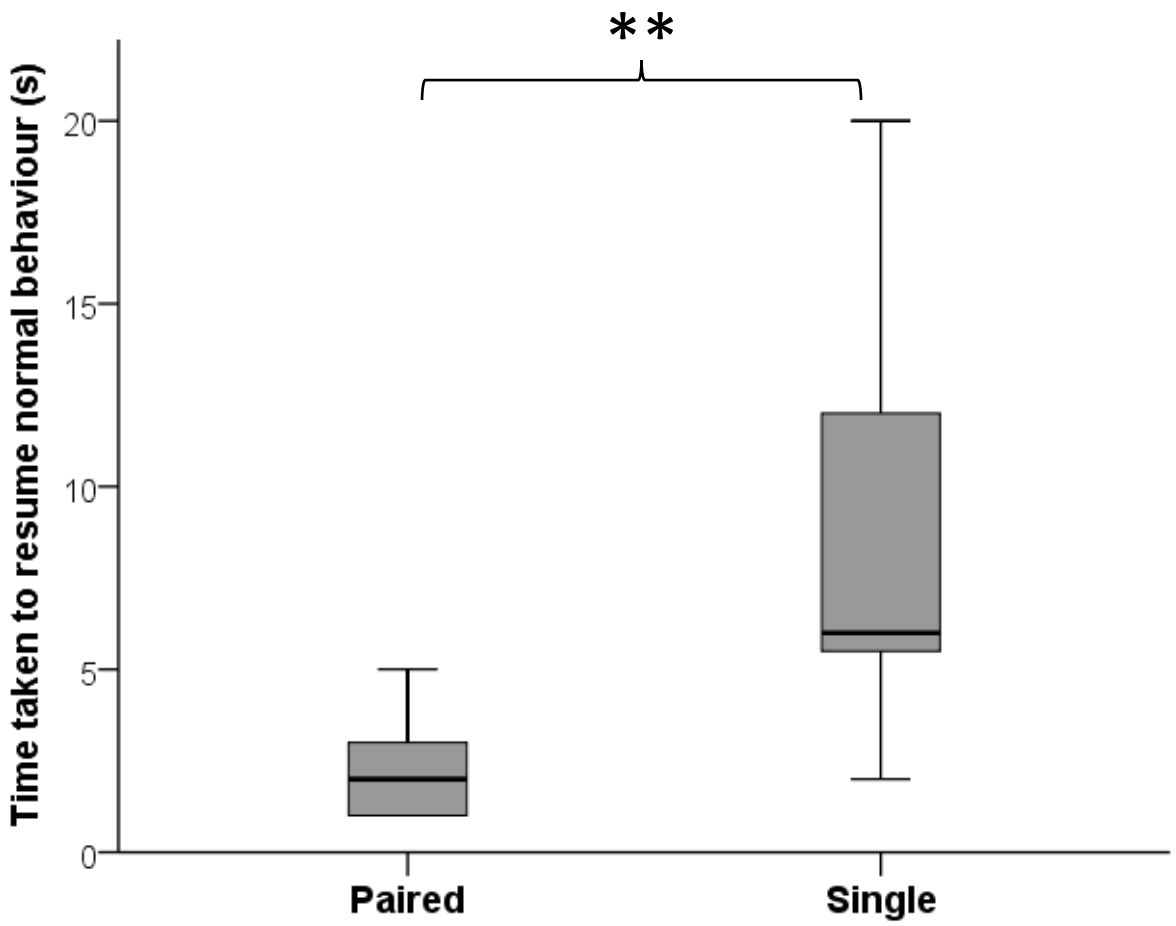

Figure 3. Time taken for paired and single housed rabbits to settle after handling. *Singletons took significantly longer to resume normal behaviour than pairs did (P = 0.036).

Tables

Table 1. Ethogram of key rabbit behaviour.

Category	Behaviour	Description	Status	Notes
Location	Front of cage	Rabbit's nearest body part is within 2 inches of the front of the pen.	State	
	Back of cage	Rabbit's furthest body part is within 2 inches of the back of the pen.	State	
	Out of sight	Observer unable to see rabbit	State	
Maintenance and investigation	Drinking	Lapping up water with tongue	Event	
	Feeding	Taking food material into mouth chewing and swallowing – from food dispenser or floor.	State	
	Grooming	Self-groom: A full body groom is usually preceded by air-boxing. The forelimbs are licked and passed over the head and ears, prior to licking/nibbling of fur over the rest of the body.	Event	
Posture	Huddled*	Two or more rabbits resting in physical contact with each other.	State	
	Compact posture	Rabbit is stationary with limbs tucked under and ears down.	State	
	Relaxed posture	Rabbit is stationary with body stretched out and limbs sprawled. Ears may be up.	State	
	Resting	Stationary in any sitting or lying posture except 'Compact', 'Relaxed' , and 'Sleep' which are defined separately.	State	
	Sleep	Lying or sitting with both eyes closed, ears usually flat against the back. Facial twitching and rapid eye movements may be seen.	State	
Possible abnormal	Bar biting	Biting the bars of the enclosure.	Event	
Social behaviour*	Aggressive behaviour	Biting, chasing, or fighting another rabbit. May include submission, parallel running, circling, tail-flagging, or urine spraying in this aggressive context.	Event	
	Sexual behaviour	Mounting and/or lordosis. May include chasing, parallel running, submission, circling, tail-flagging or urine spraying in this sexual context.	Event	
	Social behaviour	Allogrooming, bowing, nose-nose contact, or nose-tail contact, sniffing each other, or nudging each other.	Event	

The ethogram was adapted from Hawkins et al. (2008). States were recorded instantaneously at 2 min intervals, whilst Events were recorded on a one-zero schedule within the 2 min intervals. *Some behaviour was only possible for paired rabbits. See Supplementary material for full ethogram.

Table 2. Signalment and housing of single and paired rabbits.

Signalment	**Singletons (n=15)**	**Pairs (n=30 rabbits; 15 pairs)**
Sex	11 bucks (neutered); 4 does (3 spayed; 1 entire)	14 buck-doe pairs (neutered); 1 buck-buck pair (neutered)
Age (years; mean+/- S.E. (min.-max.))	1.87+/-0.43 (0.3-6)	3.85+/-0.35 (1.4-8.4)
Size category (n)	L (x3), M (x5), S (x4), XS (x3)	XL (x2), L (x3), M (17), S (x6), XS (2)
Breed	Dwarf lop (x3), Crossbreed (x3), English lop (x1), Harlequin (x1), Lionhead (x2), Lion lop (x1), Netherland dwarf (x1), Other lop (x2), Rex (x1)	Cashmere (x2), Crossbreed (x8), Dutch (x2), French lop (x1), Giant Papillon (x1), Harlequin (x1), Lionhead (x3), Netherland dwarf (x1), Netherland lop (x1), Other lop (x6), Other non-lop (x2), Rex (x2)
Proportion who arrived single at rescue	1/15	6/30
Estimated time at shelter until handling (days; median (IQR))	288 (119-378)	592 (498-994)
Enclosure size (m^2; median (IQR))	1.11 (0.93-1.45)	1.95 (1.67-4.46) [Per rabbit = 0.98 (0.84-2.23)]
Proportion of enclosures in the barn versus outside	5/15	0/15

The ages and breeds were as recorded by the relinquishing owners or estimated by the rescue centre staff. The rabbit sizes were subjectively scored by a single observer, and ranged from Extra Large (XL) to Extra Small (XS).

Table S1. Full ethogram of rabbit behaviour. States were recorded instantaneously at 2 min intervals, whilst events were recorded on a one-zero schedule within the 2 min intervals. Not all of these behaviours were ever seen, and some were only possible in paired rabbits. The ethogram was adapted from Hawkins et al. (2008).

Category	Behaviour	Description	Status	Notes
Location	Front of cage	Rabbit's nearest body part is within 2 inches of the front of the pen.	State	
	Back of cage	Rabbit's furthest body part is within 2 inches of the back of the pen.	State	
	Out of sight	Observer unable to see rabbit	State	
Maintenance and investigation	Air-boxing	Fast forward–flicking of forelimbs whilst rabbit sits upright on haunches. Usually precedes body grooming.	Event	
	Body rolling	Rabbit throws self onto ground in a sideways roll, may lie immobile in outstretched position on side with eyes half closed for some seconds after roll. Often performed as dust-bathing in the wild.	Event	
	Body stretch	Rabbit stretches body out forwards to full length, front and back legs extended. Slow movement.	Event	
	Burrowing	Rabbit using front limbs scratching and flicking bedding material, and pushing face into bedding material.	State	
	Coprophagy	Rabbit removes, chews and swallows soft, mucus-covered coprophagy pellets directly from anus.	Event	
	Defaecation	Release of faecal pellets.	Event	
	Digging	Prolonged paw-scraping at deep substrate, usually associated with burrow excavation. The substrate is thrown under and behind the body and the rabbit may turn and push the displaced spoil further back with alternate forward thrusting movements of the forepaws.	State	
	Drinking	Lapping up water with tongue.	Event	
	Feeding	Taking food material into mouth chewing and swallowing – from food dispenser or floor.	State	
	Grooming	Self-groom: A full body groom is usually preceded by air-boxing (see above). The forelimbs are licked and passed over the head and ears, prior to licking/nibbling of fur over the rest of the body.	Event	
	Sniffing	Close sniffing of object/conspecific.	Event	Sniffing conspecific

				valid for pairs only
	Scratching	Scratching at own body with a hindfoot.	Event	
	Chin marking	Rubbing the chin over an object or conspecific.	Event	Marking conspecific valid for pairs only
	Body shake	Rabbit's whole body shakes/shivers	Event	
Locomotion	Jumping	Vertical movement either onto an elevated surface or into the air.	Event	
	Running	Running – rapid forward movement achieved by alternate, fully-stretched extension of fore and hindlimbs.	Event	
	Hopping	Forward movement achieved by alternate extension of fore and hindlimbs. Distinguished from running by its slower speed and shorter distance covered per forward jump.	Event	
	Play	Head flicking – flicking head sideways. Play gambolling or 'frisky hop' – forward hopping/jumping accompanied by sideways tossing of the head/ears, shaking/twisting the body or kicking out with the feet. Rabbits may also run back/forth at some speed during this activity.	Event	
	Rearing	Sitting up on hindlimbs with both forepaws off the ground.	Event	
Posture	Huddled	Two or more rabbits resting in physical contact with each other.	State	
	Compact posture	Rabbit is stationary with limbs tucked under and ears down.	State	
	Relaxed posture	Rabbit is stationary with body stretched out and limbs sprawled. Ears may be up.	State	
	Resting	Stationary in any sitting or lying posture except 'Compact', 'Relaxed' , and 'Sleep' which are defined separately.	State	
	Sleep	Lying or sitting with both eyes closed, ears usually flat against the back. Facial twitching and rapid eye movements may be seen.	State	
Possible abnormal	Bar biting	Biting the bars of the enclosure.	Event	
	Fur pulling	Rabbit pulls mouthfuls of fur or hair from own body.	Event	
	Biting self	Rabbit opens mouth and closes it again with own skin/fur still in mouth	Event	

Communication	Low-pitched grunting	Low-pitched vocalisation. Typically heard in pursued does, sexually aroused does, sexually pursued but unreceptive does.	Event
	Screaming	Very high pitched screeching. Typically when rabbit is injured or frightened.	Event
	Thumping	Audible thumping of the ground with the hindfoot (feet), usually when alarmed but males may also foot-thump after mating.	State
Social (Pairs only)	Allogrooming	Rabbits lick the fur of another rabbit (usually around the head, particularly the ears)	Event
	Aggressive circling	Slow or rapid chasing around and around in one spot; participants may have rear end of opponent gripped between their teeth.	Event
	Biting other	Rabbit opens mouth and closes it again with another rabbit's skin/fur still in mouth	Event
	Bowing head	Head lowered, neck outstretched (sometimes with eyes partly or fully closed) towards approaching rabbit.	Event
	Chasing rabbit	Rabbit rapidly pursues another, often with tail erect.	Event
	Circling	Slow or rapid chasing around and around in one spot	Event
	Courtship circling	Male runs semi-circles, alternating around stationary or slow-moving female. Also occurs between females in single-sex groups.	Event
	Crouching	A submissive behaviour; animal 'freezes' and presses head and shoulders against ground with ears flattened.	State
	Fighting	Involves fast movements with limbs or teeth and showing of teeth between two or more rabbits, often with combatants leaping into the air/past each other.	Event
	Lordosis	Female crouching still with curved, convex spine, tail elevated and vulva visible.	Event
	Mounting	Mounting of hindquarters (or head) of conspecific.	Event
	Nose to nose approach	Two rabbits approach head on with necks outstretched and sniff nose to nose and/or nose to chin.	Event

	Nose to tail approach	One rabbit approaches another from the rear and sniffs under his/her tail (typically in the context of a male sniffing to determine the oestrous status of a female).	Event
	Nudging	Rabbit pushes nose against body or rump of conspecific.	Event
	Parallel running	Two rabbits run in parallel, with elevated gait, tail erect and at a slow pace.	Event
	Paw scraping	Rapid but brief scratching at the ground with the forepaws.	Event
	Submitting	Rabbit ceases to move and drops nose below the nose of an approaching animal.	Event
	Tail Flag	Rabbit has tail fully vertically erect towards another rabbit (typically during aggressive/courtship interaction).	Event
	Urine spray	A short jet of urine is emitted during a twist/jump action where either the whole body, or the hindlimbs alone, are lifted and the hindquarters swung around in a semi-circle. Typically, this spray is directed at another rabbit, either during courtship or an aggressive encounter.	State