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Animal 17 (2023) 100724

Contents lists available at ScienceDirect

Animal

The international journal of animal biosciences

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M. Fetiveau, D. Savietto, V. Fillon, C. Bannelier, S. Pujol, L. Fortun-Lamothe *

GenPhySE, Université de Toulouse, INRAE, ENVT, 31326 Castanet-Tolosan, France

ARTICLE INFO

Article history:
Received 13 September 2022
Revised 23 January 2023
Accepted 24 January 2023
Available online 2 February 2023

Keywords:
Corticosterone
Free-range area
Oryctolagus cuniculus
Shelter
Welfare

ABSTRACT

Providing rabbits with a grassy outdoor area allows them to express a broad variety of specific behaviours such as grazing where grazeable herbage persists. However, rabbits that graze are also exposed to external stressors. Controlled outdoor access time may help preserve the grassland resource, while a hiding place may offer the rabbits a secure space. We focused on rabbit growth, health and behaviour according to outdoor access time and the presence of a hideout on a 30-m^2 pasture area. We divided 144 rabbits into four groups (group of rabbits with 8 hours per day (H8) of access to pastures provided with an hideout (Y) (**H8Y**): n = 36; group of rabbits with 8 hours per day (H8) of access to pastures unprovided with an hideout (N) (**H8N**): n = 36; group of rabbits with 3 hours per day (H3) of access to pastures provided with an hideout (Y) (**H3Y**): n = 36; group of rabbits with 3 hours per day (H3) of access to pastures unprovided with an hideout (N) (**H3N**): n = 36) that differed in access time (**H8**, four replicates, eight hours a day from 0900 h to 1700 h; and **H3**, four replicates, three hours a day from 0900 h to 1200 h) and the presence of a hideout (presence of an hideout on the pasture (**Y**), four replicates, with a roof-shaped wooden hideout; and absence of an hideout on the pasture (**N**), four replicates, without). Rabbit growth and morbidity were measured weekly for each rabbit from 34 to 76 days of age. Rabbit behaviour was assessed on days 43, 60 and 74 by direct visual scanning. Available grassy biomass was evaluated on days 36, 54 and 77. We also measured the time rabbits took to enter and exit the mobile house and the level of corticosterone accumulated in their hair during the fattening period. There were no between-group differences in live weight (on average, 2 534 g at 76 days of age) and mortality rate (18.7%). The rabbits expressed a broad variety of specific behaviours, with grazing being the most frequent (30.9% of all the observed behaviours). Foraging behaviours including pawscraping and sniffing were more frequently observed in H3 rabbits than H8 rabbits (1.1 vs 0.3% and 8.4 vs 6.2%, respectively; $P < 0.05$). There was neither an access-time nor hideout presence effect on rabbit hair corticosterone levels or time to exit and enter the pens. Patches of bare ground were more frequent in H8 pastures than in H3 pastures (26.8 vs 15.6%, respectively; $P < 0.05$). Over the whole growing period, the biomass intake rate was higher in H3 than H8 and higher in N than Y (1.9 vs 0.9 g/rabbit/h and 1.8 vs 0.9 g/rabbit/h, respectively; $P < 0.05$). In conclusion, restricted access time tended to slow the reduction of the grass resource but had no detrimental effects on rabbit growth or health. Rabbits facing restricted access time adapted their grazing behaviour. A hideout helps rabbits cope with external stressors.

Implications

Rabbits are herbivores, and access to an enriched, grassy outdoor space enables them to express a diverse range of specific behaviours such as grazing or foraging. It is important that the grass resource remain available throughout the fattening period so as not to restrict the expression of these specific behaviours. Managed access time had a moderate influence on preservation of the grass resource as it gave the rabbits a very strong motivation to graze. Enrichment of the living environment with a hideout could help maintain the attractiveness of a pasture, regardless of the state of the grass resource.

Introduction

Indoor farming systems keep animals in environments that are highly restricted in terms of size and complexity compared to their wild counterparts (McPhee and Carlstead, 1996). Cage-based housing systems used in rabbit husbandry restrain animal locomotion

* Corresponding author.
E-mail address: laurence.lamothe@inrae.fr (L. Fortun-Lamothe).

https://doi.org/10.1016/j.animal.2023.100724
1751-7311/

(Lehmann, 1987) and constrain the expression of specific behaviours such as grazing (Thompson, 1951; Mykytowycz and Rowley, 1958) and foraging (Prebble et al., 2015) that are ubiquitous in herbivorous species like rabbits. Caged rabbits are therefore likely to experience frustration because their behavioural needs are not met. Elevated corticosterone levels and stereotypic behaviours are often a sign of frustration (Latham and Mason, 2010) and can lead to stress that, in turn, affects growth and induces disease (Wood-Gush et al., 1975). Expectations are often inferred from anticipatory behaviours (Anderson et al., 2020). Anticipatory behaviours may indicate a positive emotional state in readiness for a reward (Rolls, 2005). They are expressed by an arousal of activity and spatial proximity to where the reward is presented to the animals (Anderson et al., 2015). If we define welfare as the absence of negative emotions and the presence of positive emotions (Boissy et al., 2007), there is a strong rationale for providing rabbits with environmentally enriched and species-adapted living conditions.

A grazing area meets rabbits' physiological and behavioural needs. Rabbits are herbivores and thus show a strong dietary preference for grass over pellets (Leslie et al., 2004), which also improves their dental health and intestinal activity (Kamphues, 2001). In the wild, however, rabbits mainly live in diverse spaces that offer grass to feed on as well as trees, bushes and scrubs to take refuge and hide from predators (Moreno et al., 1996; Beja et al., 2007; Lombardi et al., 2007). In husbandry conditions, rabbit welfare, health and growth can be improved by ensuring that the outdoor layout does not restrict the behavioural patterns of the rabbits when outside.

Our previous research showed that growing rabbits given access to grassy pastures spent most of their time near the entrance of the rabbit house, especially in the first two weeks after weaning (Fetiveau et al., 2021). The areas closer to the house are thus more prone to soiling, which can promote parasitic infestations like *Eimeria* sp. In wild rabbits, Lombardi et al. (2007) showed that enrichment of the outdoor area with refuges leads to an even distribution of the animals on the pasture. In poultry, Fanatico et al. (2016) showed that chickens used the range more fully if it was provided with a constructed enrichment. Additionally, Hegelund et al. (2005) observed more hens on pasture and more hens away from the area immediately outside the hen house when pasture had artificial cover compared to uncovered pasture. Taken together, these results suggest that providing pastures with shelters could be a promising way to stimulate rabbits to use the whole pasture area, thus preventing the accumulation of faeces close to the mobile house and therefore limiting parasitism, as suggested by Van de Weerd et al. (2009). Shelters could also keep the pastures attractive to the rabbits, regardless of the amount of grass left.

Mykytowycz and Rowley (1958) showed that rabbits spend between 2.5 and 6 hours a day grazing. Providing rabbits with a sufficient pasture area would be the most obvious solution to enable them to consistently freely express grazing behaviour over time (Fetiveau et al., 2023), but it relies on farms with enough land to accommodate all the animals, including for plot rotations. Alternatively, reducing stocking density can preserve available grass biomass (Fetiveau et al., 2021). Limiting access time to pasture is also another successful solution to prevent degradation of the pasture resource (Pérez-Ramírez et al., 2008) since the quantity of herbage consumed by grazing animals depends on grazing time, bite rate and intake per bite (Holmes, 1989). Restricted access time to pasture has been intensively studied in ruminants. Newman et al. (1994) showed that grazing animals have the ability to adapt their intake rate via greater motivation to graze when outdoor access time is restricted. For instance, in cows, when access time to pastures was decreased from 8 to 4 hours a day, the proportion of time spent grazing, grass intake per minute and intake per bite all increased (Pérez-Ramírez et al., 2008; Kennedy et al., 2009). It would therefore be instructive to test whether rabbits adapt their grazing behaviour when outdoor access time is restricted. In contrast to cows, rabbit grazing behaviour has been under-researched. Thompson (1951) showed that grazing rabbits performed 120 jaw movements per minute during chewing, and Legendre et al. (2019) showed that rabbits are able to ingest up to 40% of their live weight in grass every day.

This study focused on the effects of access time and the presence of a hideout on the behaviour, stress levels, health status and growth traits of weaned rabbits. We determined whether pastures environmentally enriched with a hideout (a) are more attractive to rabbits, regardless of the amount of grass available; (b) reduce the stress of rabbits as it better mimics their natural environment; and (c) favour health, reducing the risk of parasitic infestation by encouraging the animals to explore the entire surface of the pasture, thus spreading droppings more evenly over the pasture. We also determined whether restricted access time to pastures (a) preserves the grassy biomass until the end of the fattening period, thus enabling rabbits to continuously graze since grazing is the major expressed behaviour of this species; (b) induces frustration, leading to higher stress; and (c) improves growth since rabbits spent more time resting in the mobile house.

Material and methods

Animals and experimental design

A total of 144 rabbits (crossbred '1001' × '1777' INRAE genetic types) of both sexes (50% of males and 50% of females) were reared for 44 days as of weaning (34 days of age; 25th May 2021) up to 76 days of age (7th July 2021). Before weaning, the rabbits were housed in wire cages (L × W × H: 90 × 90 × 60 cm) by litter. The cages were provided with a platform and a gnawing stick. After weaning (during the present experiment), rabbits were housed in a 30-m^2 mobile house placed in a pasture and equipped with eight 2-m^2 roofless pens, as described by Fetiveau et al. (2021). Each pen was equipped with two platforms (W × L: 35 × 100 cm) and a hayrack (W × L × H: 24 × 41 × 48 cm) placed on the side opposite the feeder, between the two platforms. The longitudinal walls of the mobile shed had four hatches (W × H: 39 × 42 cm) designed to allow access to the pastures in front of each pen (see Supplementary Fig. S1). No artificial lighting was provided inside the mobile house. The outdoor area was protected from predators by a three-wire electric fence. The pastures were limited on the outside edge with flexible electric netting (H: 65 cm) and a sweet chestnut (*Castanea sativa*) fence (H: 100 cm) between each paddock, with each log set 2–3 cm apart. The pastures were in a meadow sown in 2016 with pure fescue (*Festuca arundinacea*) and since covered mainly with *Lolium perenne*, *Trifolium repens* and *Crepis setosa*, but with a substantial amount of *Rumex crispus* and *Hordeum murinum* on each pasture (not quantified).

At weaning, rabbits of both sexes were evenly distributed in a 2 × 2 factorial design, including access time to a 30-m^2 pasture area (8 hours a day from 0900 h to 1700 h: **H8,** or 3 hours a day from 0900 h to 1200 h: **H3**) and the presence (**Y:** yes) or absence (**N:** no) of a wooden A-frame hideout (W × L × H: 75 × 63 × 40 cm; see Supplementary Fig. S2). In total, there were four experimental groups (group of rabbits with 8 hours per day (H8) of access to pastures provided with an hideout (Y) (**H8Y**): n = 36, group of rabbits with 3 hours per day (H3) of access to pastures provided with an hideout (Y) (**H3Y**): n = 36, group of rabbits with 8 hours per day (H8) of access to pastures unprovided with an hideout (N) (**H8N**)**:** n = 36, group of rabbits with 3 hours per day (H3) of access to pastures unprovided with an hideout (N)

(**H3N**): n = 36) with two repetitions of 18 rabbits per group. Animal density was nine rabbits/m^2 in the pens and 0.6 rabbits/m^2 on the pastures (18 rabbits on 2 m^2 or 30 m^2, respectively). On weekends, all groups had three hours of access to the pasture (from 0900 h to 1200 h). Each hatch between the indoor area and the pasture was kept open during the outdoor access time for the free movement of animals. Since rabbits are crepuscular animals, we chose to only allow outdoor access in daylight in order to gain better knowledge of their motivation to go outside. Experimenters made voice signals (i) when they entered the mobile house to open the hatches, and (ii) when they moved from the bottom of the paddocks to the entrance of the rabbit house to make the rabbits enter. Rabbits were given access to the pastures from days 40 to 76. Throughout the experiment, the rabbits were fed *ad libitum* with a pelleted diet (STABI-FIBRE, Terrya, Rignac, France; 15.6 MJ of gross energy per kg DM, 15.1 CP, 3.0 fat, 55.3 NDF, 32.3 ADF and 6.7% ADL on a DM basis) and with hay (15.5 MJ of gross energy per kg DM, 5.1% CP, 59.3% NDF, 34.7% ADF and 7.2% ADL on a raw basis). The diet contained wheat bran, sugar beet pulp, sunflower cake, dehydrated alfalfa, barley, sunflower seed hull, beet molasses, rapeseed cake, extruded peas, extruded flaxseed, rapeseed oil and additives (minerals: calcium carbonate, sodium chloride, dicalcium phosphate; vitamins A, B1, D3, E; micronutrients: Co, Cu, Fe, Mn, Se, Zn; organic acids). The animals were individually weighed once a week between days 34 and 76. Pelleted feed and hay intake per pen-paddock were measured weekly.

Ambient parameters and grassland areas

The temperature and humidity inside and outside the shed were recorded daily with a probe (Omega OM-CP-RHTEMP101A). Rainfall and wind speed were also monitored daily from the INRAE CLIMATIK platform (https://intranet.inrae.fr/climatik/) managed by the AgroClim laboratory (Avignon, France). Herbage height was measured in each paddock with a grazing stick at 25 points along two transects per paddock on days 36, 54 and 77. Botanical composition, defined as the proportion of legumes or grass in eight 0.25-m^2 plots, was also measured on days 36, 54 and 77. To estimate plant biomass in the pastures, four 0.25-m^2 plots were sampled at a distance of 0.5, 2, 4 and 6 m from the exit hatch along two transects on days 36, 54 and 77, by cutting all the grass inside the plots at a height of 2 cm from the ground. Samples were pooled and placed in micro-perforated bags and stored at 4 °C. The samples were then analysed using the methods described by the EGRAN (2001) group as most appropriate for rabbit nutritional experiments, i.e., DM (48 h at 60 °C; ISO 6496:1999 method), ash, CP (N $\times$ 6.25, Dumas method, ISO 16634:2004 method) and fibres (ADL, ADF and lignin; Van Soest et al., 1991).

Rabbit exit time

Throughout the experiment, the time the first rabbit exited the mobile house to go to the pasture was measured at each hatch opening (at 0900 h, Monday to Sunday). Additionally, when rabbits were aged 65 days, the sequence beginning with the experimenter entering the mobile house to the opening of the hatch of each pen was video-recorded to identify signs of frustration. The recording was analysed using Boris software (Friard and Gamba, 2016) to measure the spatial distribution of the animals in the pens (animals were counted on the floor between the platforms, on the floor under the platform near the hatch, on the floor under the platform opposite the hatch, on the platform near the hatch, and on the platform opposite the hatch), and to describe their behaviours using the *ad libitum* sampling method (Altmann, 1973).

Rabbit entrance time

Each time a hatch was locked (1200 h for H3 or 1700 h for H8 on Monday to Friday, and at 1200 h on Saturday and Sunday), the time taken to put all the rabbits back in their pens was measured in order to evaluate whether the animals showed resistance to entering the pen (interpreted as a possible sign of frustration). The rabbits were herded back into their pens by one experimenter who entered the paddocks and clapped her/his hands while speaking to the animals. A second experimenter then closed the hatch doors.

Spatial distribution of rabbits

Spatial distribution of the rabbits in the pens and on the pastures was evaluated four times a week (twice a day for two days, i.e., at 1000 and 1600 h) for six weeks. We counted the number of rabbits in (i) three areas inside the pens: on the platforms; on the ground floor between the two platforms; and under the platforms. We also counted the rabbits in (ii) five areas in the paddocks: from 0 to 2.5 m from the exit hatch; from 2.5 to 5.0 m; from 5.0 to 7.5 m; and from 7.5 to 10.0 m, and in a 20-cm radius around the hideout, which was placed at 6 m from the hatch.

Behavioural evaluation

Behaviour of animals was assessed for 10 minutes using the scan sampling method (Altmann, 1973) with direct simultaneous observations inside the mobile shed and outside on pastures (the time interval between two scans was 2 sec). Observations were made in the morning (between 0900 and 1100 h, with all groups having outdoor access) and in the afternoon (between 1500 and 1700 h with only group H8 having outdoor access) on rabbits aged 43, 60 and 74 days old. We recorded 22 different behaviours, classed into six categories (see Supplementary Table S1), as described by Gunn and Morton (1995) and Coda et al. (2020): moving (Hopping and Walking); maintenance (Grazing, Eating hay, Eating pellets, Resting, Drinking, Gnawing); comfort (Stretching, Yawning, Grooming); exploration and alertness (Pawscraping, Rearing, Sniffing, Stamping, Chinning, Watching); interaction (between two or more rabbits: Allogrooming, Side-by-side, High-speed chase, Nose-to-nose); and Capering (happy leap known as 'binky'). All these behaviours are not mutually exclusive and can overlap each other. The results are expressed as the percentage of total observations. The number of times rabbits entered and exited the hideout and the behaviours of rabbits under the hideout were assessed on 30-minute video-recording sequences filmed between 0930 and 1000 h on days 42, 56 and 67.

Hair corticosterone levels

A patch of hair (5 $\times$ 5 cm) was shaved with small clippers on all the rabbits from the back just behind the shoulder blades at 40 days of age, and the hair was then discarded. Then, at 71 days of age, around 250 mg of hair was collected from 38 rabbits (50% of each sex and each group) by shaving following the same protocol. The samples were stored at −20 °C until the extraction of corticosterone. The method used was an adapted ELISA corticosterone immunoassay: we used a competitive immunoassay kit designed for the quantitative measurement of salivary cortisol (Salimetrics® Cortisol Enzyme Immunoassay kit) following the procedure developed by Salimetrics. Optical density was read on a Glomax spectrophotometer (Promega) at 450 nm and 490 nm. The concentration of each sample was determined by interpolation using a 4-parameter non-linear regression curve fit (Myassays software) and converted into pg/mg considering dilution factors.

Rabbit health

The health status of animals was checked once a week between days 34 and 76 (healthy was defined as having no sign of disease, thinness, digestive problem, abscess). Mortality was monitored daily. Coccidia oocysts were counted on 9 grams of faeces taken once a week in each pen. Samples were collected on a steel shelf set in place under one of the two platforms of each pen, then stored at 5 °C for no more than 3 days before analysis according to the McMaster method (Gibbons et al., 2005).

Statistical analysis

All analyses were performed using R statistical software, version 4.0.3 (R Core Team, 2020). Mathematical equations of the statistical models described below are available in Supplementary Table S2.

Analysis of each variable detailed below used a compound symmetry covariance structure of the R matrix. Herbage height data were analysed using independent linear models for each day of measurement. The proportion of grass, legumes, bare ground and stems was analysed with a proportion test for each day of measurement. Biomass available in pastures on days 36, 54 and 77 was analysed using a linear model that included access time (two levels: H3 and H8), hideout presence (two levels: Y and N) and their interaction as fixed effects, and the pen as a random effect, the pen being the experimental unit. The biomass intake rate was analysed using a mixed linear model that included access time (two levels: H3 and H8), hideout presence (two levels: Y and N) and their interaction as fixed effects, and the pen (experimental unit) as a random effect. Live weight of rabbits at 34 and 76 days of age and average daily gain between days 34 and 76 were analysed with a mixed model that included access time (two levels: H3 and H8), hideout presence (two levels: Y or N) and their interaction as fixed effects, and the animal (experimental unit) as a random effect. Mortality between days 34 and 76 days of age was analysed as a binary trait (0 = dead and 1 = alive) using a logistic regression model with access time, hideout presence and their interaction as fixed effects, and the pen (experimental unit) as a random effect. Spatial distribution data were analysed using a negative binomial regression that included access time, hideout presence and their interaction as fixed effects, and the pens (experimental unit) as a random effect for only the morning period. The proportions correspond to the total number of rabbits observed at each site over the total number of observations (pens + pastures), all ages combined. The rabbit hatch entrance and exit time data were analysed using a negative binomial model that included access time, hideout presence, age (five levels: 40–46 days, 47–53 days, 54–60 days, 61–67 days, and 68–75 days) and their interaction as fixed effects, and pens (experimental unit) as a random effect. The number of times rabbits entered and exited the hideout was analysed with a generalised linear model with a Quasi-Poisson link function that included rabbit age (three levels: 42, 56 and 67 days of age), access time (two levels: H3 and H8) and their interaction as main effects. Behavioural data were analysed with a generalised linear mixed model using Template Model Builder that included access time, hideout presence and their interaction as fixed effects, and pens (experimental unit) as a random effect for each observation site (pastures or pens) and for each period of observation (morning or afternoon). Time of day (morning or afternoon) of the behavioural evaluation was analysed independently since only the H8 group was observed on pastures in the afternoon. Behavioural data under the hideout were analysed using a negative binomial generalised linear model with access time as the main effect at each age of observation (42, 56 and 67 days of age). Hair corticosterone levels were analysed using a linear mixed effect model that included access time, hideout presence and their interaction as fixed effects, and the pens (experimental unit) as a random effect. Coccidia oocyst count was analysed using a negative binomial model that included access time, hideout presence, rabbit age (six levels: 37, 44, 51, 58, 65; and 72 days old) as fixed effects, and the pens (experimental unit) as a random effect.

Results

Environmental conditions and herbage allowance

Average indoor and outdoor temperatures during the experiment were 22.8 °C (min 14.5 °C and max 34.1 °C; (Supplementary Fig. S3A) and 20.5 °C (min 7.1 °C and max 33.1 °C; Supplementary Fig. S4A), respectively. Average indoor and outdoor relative humidity during the experiment were 65.8% (min 30.1% and max 95.7%; Supplementary Fig. S3B) and 66.4% (min 15.6% and max 96.6%; Supplementary Fig. S4B). At each age, the mean amount of grazeable biomass available was similar between pastures (on average, 6.0 kg DM/pasture at day 36, 3.4 kg DM/paddock at day 54, and 3.0 kg DM/pasture at day 77; Supplementary Fig. S5). Chemical composition (pooled samples) of the meadow was 40.7% DM, 4.4% CP, 20.1% NDF, 10.5% ADF, 2.4% lignin and 5.0% ash on a raw basis. Average overall herbage height was 18.2 ± 10.1 cm at day 36, i.e., four days before rabbits were given outdoor access (Table 1), and was similar between treatment groups. Botanical composition of pastures differed between H3 and H8 at day 36, i.e., 60.0 vs 72.5% grass and 37.5 vs 26.2% legumes between H3 and H8, respectively ($P < 0.05$). Between days 36 and 77, the proportions of grass and legumes decreased by 3.2% ($P = 0.82$) and 45.1% ($P < 0.05$) in H3 pastures, by 37.9% ($P < 0.05$) and 26.3% ($P = 0.18$) in H8 pastures, by 28.1% ($P < 0.05$) and 29.8% ($P = 0.11$) in Y pastures, and by 15.4% ($P = 0.11$) and 43.1% ($P < 0.05$) in N pastures. The proportion of bare ground increased between day 36 and day 77 from 0.0 to 15.6% in H3 pastures ($P < 0.05$) and from 0.6 to 26.8% in H8 pastures ($P < 0.05$). The proportion of bare ground in Y and N pastures increased from 0.6 to 21.9% ($P < 0.05$) and from 0.0 to 20.6% ($P < 0.05$), respectively. There was no effect of access time × hideout interaction on biomass intake rate ($P = 0.09$). Biomass intake rate between day 40 and day 76 was higher in N than in Y (1.8 vs 0.9 DM/rabbit/hour, respectively; $P < 0.05$; Fig. 1A) and higher in H3 than in H8 (1.9 vs 0.9 g DM/rabbit/hour, respectively; $P < 0.05$; Fig. 1B).

Animal traits

The mortality rate reached 18.7% over the whole growing period and showed no effect of access time, hideout presence or access time × hideout interaction (Table 2). All the rabbits that died had digestive problems (epizootic rabbit enteropathy). Death rates peaked when rabbits were aged between 56 and 62 days (56.5%). All the live rabbits that reached 76 days old were healthy, regardless of the experimental group. Live weight of rabbits at 34 and 76 days of age was similar, regardless of access time and hideout presence (on average, 1 019 ± 115 g at day 34, and 2 534 ± 160 g at day 76). Likewise, the average daily gain between day 34 and day 76 (on average, 36.1 ± 2.6 g/d) was not dependent on access time or hideout presence. There was no statistical effect of access time or hideout presence on hair corticosterone levels (on average, 3.2 pg corticosterone per mg hair; see Supplementary Fig. S6). The number of oocysts per gram of faeces (OPG) was only affected by rabbit age ($P < 0.05$; Fig. 2). OPG peaked at day 44 (26 059 OPG) and then continuously decreased until day 65 (2 533 OPG) before increasing again up to day 72 (3 183 OPG).

Table 1
Means for herbage height (cm) and percentage of grass, legumes, bare ground and stems in the pastures according to rabbits grazing-area access time (H3: 3 hours a day, or H8: 8 hours a day), the presence of a hideout (Y: with a hideout; or N: no hideout) and day of measurement (36, 50 or 77 days).

	Access time		Hideout			*P*-value		
Item	H3	H8	Y	N	RSD	Access time	Hideout	Access time × Hideout
Herbage height[†] (cm) at								
Day 36	17.3	19.1	17.5	18.9	10.1	0.11	0.19	0.61
Day 54	10.0	9.5	9.9	9.6	7.7	0.54	0.73	0.11
Day 77	4.4	3.2	4.6	3.0	3.4	<0.05	<0.05	<0.05
Grass[‡] (%) at								
Day 36	60.0	72.5	71.2	61.2	NE[1]	<0.05	0.07	
Day 54	46.9	54.4	50.0	51.2	NE	0.22	0.91	
Day 77	58.1	45.0	51.2	51.8	NE	<0.05	1.00	
Legumes (%) at								
Day 36	37.5	26.2	27.5	36.2	NE	<0.05	0.12	
Day 54	42.5	26.8	33.7	35.6	NE	<0.05	0.81	
Day 77	20.6	19.3	19.3	20.6	NE	0.88	0.89	
Bare ground (%) at								
Day 36	0.0	0.6	0.6	0.0	NE	1.00	1.00	
Day 54	1.2	5.0	5.0	1.2	NE	0.11	0.11	
Day 77	15.6	26.8	21.9	20.6	NE	<0.05	0.89	
Stems (%) at								
Day 36	0.0	0.0	0.6	2.5	NE	1.00	0.37	
Day 54	9.4	13.7	11.2	11.9	NE	0.29	1.00	
Day 77	5.6	8.7	7.5	6.9	NE	0.39	1.00	

[†] Means for herbage height did not consider the number of measurement points with bare ground (day 36: 0 points for H3, 1 point for H8, 1 point for Y, and 0 points for N; day 54: 2 points for H3, 8 points for H8, 8 points for Y, and 2 points for N; day 77: 25 points for H3, 43 points for H8, 35 points for Y, and 33 points for N).
[‡] Proportion of grass in relation to the number of measurements for each group (40 measurement points for each 30-m^2 pasture area). The interactional effect could not be calculated since a proportional test was used.
[1] NE: not estimable.

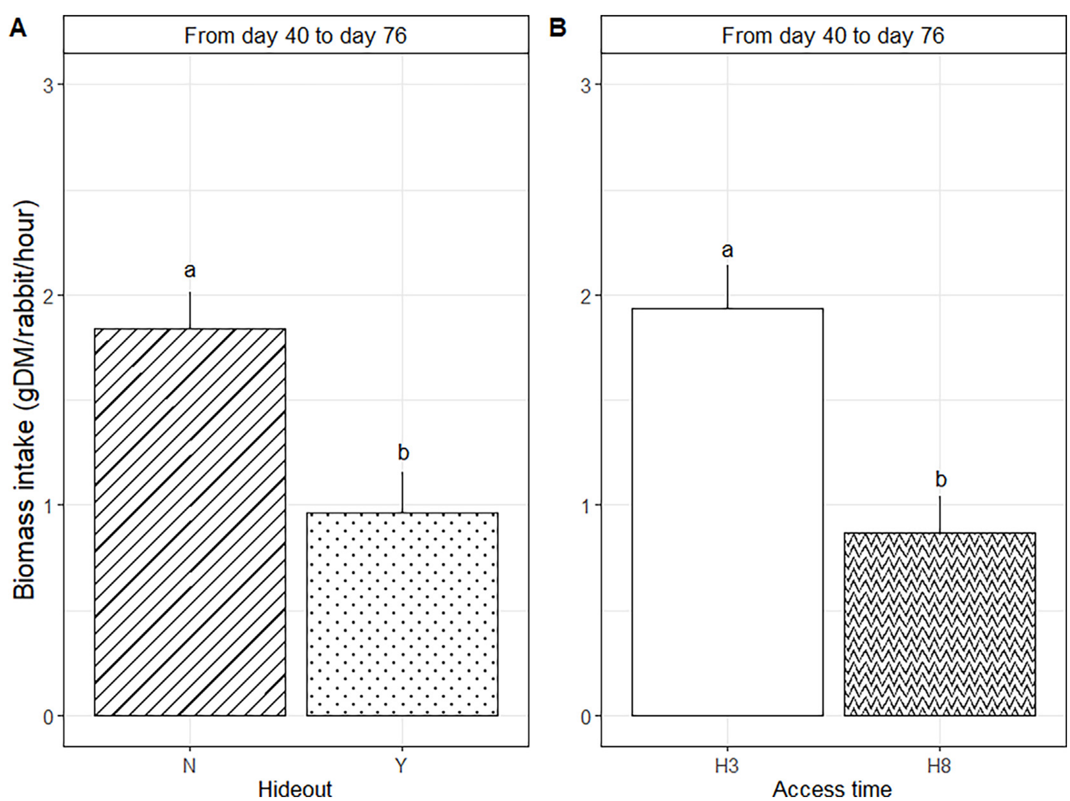

Fig. 1. Intake of g of biomass per rabbit and per hour according to hideout (Y: with a hideout; N: no hideout: N) (**A**) and access time (H3: 3 hours a day, or H8: 8 hours a day) (**B**) between 40 and 76 days of age. Black lines represent SE. Bars with different letters (a, b) differ significantly at $P < 0.05$.

Pelleted feed and hay intake

Over the whole period, the average feed intake was 115.1 g/day/rabbit and the average hay intake was 8.3 g/day/rabbit. There were no differences in intakes according to access time (on average, 115.7 vs 114.4 g/day/rabbit for pellet feed and 8.9 vs 7.7 g/day/rabbit for hay between H3 and H8, respectively) or hideout presence (on average, 115.7 vs 114.5 g/day/rabbit for pellet feed and 8.8 vs 7.8 g/day for hay between Y and N, respectively). There was a peak in feed and hay intake at six weeks postweaning (on average,

Table 2
Means for rabbit growth and mortality traits according to access time (H3: 3 hours a day, or H8: 8 hours a day) and the presence of a hideout (Y: with hideout; N: no hideout).

Item	Access time		Hideout		RSD	P-value[†]	
	H3	H8	Y	N		Access time	Hideout
Number of rabbits at 34 days of age	72	72	72	72			
Live weight (g) at 34 days of age	1 018	1 020	1 018	1 020	115.8	0.91	0.94
Number of rabbits at 76 days of age	59	59	58	60			
Live weight (g) at 76 days of age	2 536	2 531	2 555	2 511	160.5	0.88	0.14
ADG[‡] (g/d) between 34 and 76 days of age	36.0	36.0	36.4	35.7	2.6	0.99	0.31
Mortality (%) between 34 and 76 days of age (%)	18.1	18.1	19.4	16.7	NE[1]	0.83	0.83

[†] The interaction between access time and hideout was not significant.
[‡] Average daily gain.
[1] NE: not estimable.

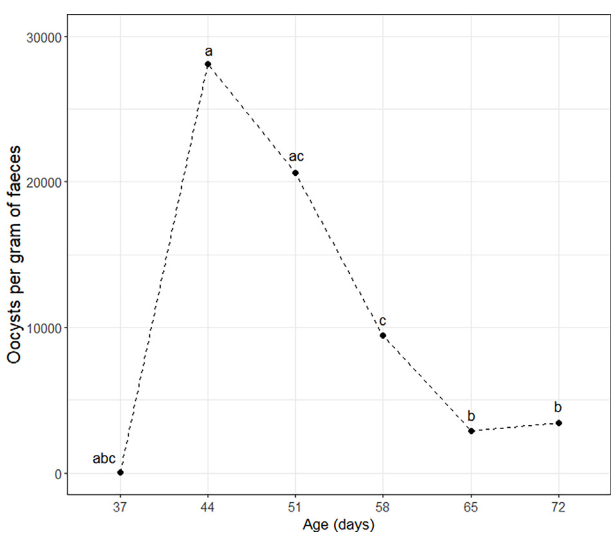

Fig. 2. Dynamics of oocyst counts (oocysts per gram of faeces) in rabbit faeces between 37 and 72 days of age in all groups combined. Values with different letters (a, b, c) differ significantly at $P < 0.05$.

155.7 g/day/rabbit and 11.6 g/day/rabbit, respectively) (see Supplementary Fig. S7). Note, however, that a large amount of hay fell under the pens and was wasted, which means the real intake estimate was biased and thus warrants caution.

Behavioural evaluation

Spatial distribution

There was no effect of access time or hideout presence on the spatial distribution of rabbits (Table 3). Throughout the whole experiment, rabbits were more frequently observed outside on pastures than inside the mobile house, i.e., in the pens, in the mornings when both the H3 and H8 groups had outdoor access (66.8 vs 33.2%, respectively; descriptive statistics only). When they were outside on pastures, rabbits were observed more frequently in the first 2.5 m from the exit hatch (38.1%), followed by the [2.5; 5 m[9.4%), [7.5; 10 m] (17.2%) and then [5; 7.5 m[intervals (11.8%). The hideout provided (Y group) attracted little use (on average, 11.5% of the outdoor observations). Inside the mobile house in the pens, rabbits were more frequently observed in the floor area below the platforms (80.8%) than on the floor between platforms (15.5%) or on top of the platforms (3.6%).

In the afternoon, only H8-group rabbits had access to outside pasture, but they were more frequently observed inside the pens than outside on pastures (on average, 72.7 vs 27.3% of observations inside vs outdoors; descriptive statistics only, data not shown). When in the pens, the H8 rabbits were more frequently observed in the floor area below the platforms (on average, 79.2% of the observations) than in other in-pen areas. When outside, they were more frequently observed in the first 2.5 m from the exit hatch (on average, 14.6% of observations) than other outdoor areas, and when they had a hideout available (H8Y group), the hideout was the second most-used area after the first 2.5 m from the hatch (on average, 19.5% of observations).

Rabbit hatch exit and entrance time

Mean time to exit the hatch over the whole experimental period was 9.5 sec. The time rabbits took to go outside at each hatch opening and the time they took to go back into their pens at each hatch closing varied with age ($P < 0.05$), regardless of access time or hideout presence. The longest time to exit was recorded between days 40 and 46, at an average of 45.2 s, and the shortest time to exit was recorded between days 68 and 75, at an average of 2.5 sec (Fig. 3A).

Table 3
Means for spatial distribution of rabbits (expressed as the frequency of total observations) according to access time (T) (H3: 3 hours a day, or H8: 8 hours a day) and the presence of a hideout (H) measured in the morning between 42 and 69 days of age.

Distribution of rabbits	Access time		Hideout		RSD	P-value[†]	
	H3	H8	Y	N		Access time	Hideout
Zones inside the mobile house							
Between platforms (%)	5.3	5.4	4.9	5.8	NE[1]	0.33	0.89
Below platforms (%)	22.9	19.9	20.1	22.7	NE	0.46	0.42
Above platforms (%)	0.7	1.2	0.6	1.5	NE	0.75	0.16
Zones outside							
[0; 2.5 m[[‡] (%)	25.6	19.9	20.9	24.4	NE	0.21	0.57
[2.5; 5 m[(%)	13.8	15.9	15.8	13.9	NE	0.33	0.21
[5; 7.5 m[(%)	5.7	11.2	5.3	12.1	NE	0.39	0.22
[7.5; 10 m] (%)	9.5	16.3	9.0	17.1	NE	0.67	0.36
Under the hideout (%)	8.9	4.3	–	–	NE	0.86	
Near the hideout (%)	4.8	9.5	–	–	NE	0.79	

[†] The interaction between access time and hideout was not significant. [‡]Distance from the hatch.
[1] NE: not estimable.

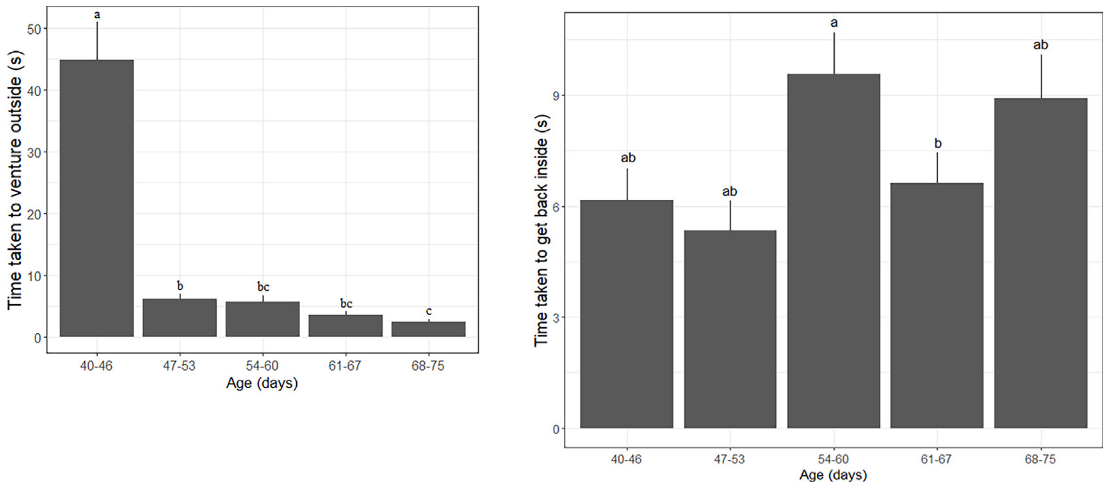

Fig. 3. Time (s) to go outside on pastures (**A**) and to enter the pens (**B**) according to access time (H3: 3 hours a day, or H8: 8 hours a day), hideout (Y: with a hideout; N: no hideout: N) and age of rabbits. Black lines represent SE. Bars with different letters (a, b) differ significantly at $P < 0.05$.

Mean time to enter the hatch over the whole experimental period was 7.4 sec. The longest time taken to herd the rabbits back into the pens was 9.7 sec between days 54 and 60, and the shortest time was 5.3 sec between days 47 and 53 (Fig. 3B).

For the hatch exit measurement, the time it took for the experimenter to enter the mobile house and open each hatch meant that rabbits had to wait between 15 sec to exit the first pen and up to 3 min for the last pen to be freed. When the experimenter stood in front of each pen before releasing the rabbits, the percentage of rabbits found on the floor near the hatch was 74.3% (for each pen). There, they expressed behaviours related to exploration and locomotion such as watching (38.0% of observations), hopping (22.3% of observations), sniffing (15.7% of observations), walking (14.0% of observations) and rearing (9.9% of observations) (data not shown).

Dynamics of hideout use

The number of entries to and exits from the hideout showed no access-time effect. On the contrary, it was influenced by the rabbit age effect (see Supplementary Fig. S8). Weather conditions (temperature, wind and storm) and pasture state regarding cover with grass may have been a stronger factor than age but could not be distinguished in our study. On average, rabbits entered and exited the hideout 1.3 times per minute at day 42 compared to 0.3 times per minute on day 56 ($P = 0.32$), and 5.9 times per minute on day 67 ($P < 0.05$). They mostly made dynamic use of the hideout, meaning that they used it as a fleeting passage. The mean number of rabbits under the hideout during observation sessions was 0.4 (min 0 and max 3) on day 42, 0.8 (min 0 and max 3) on day 56, and 0.7 (min 0 and max 9) on day 67.

Comparison of rabbit behaviour on pastures and in the pens

On pastures, in the morning and regardless of the observation day, walking, resting and rearing were more frequent in H8 rabbits than H3 rabbits (4.0 vs 3.5%, 17.1 vs 5.9% and 10.5 vs 7.2%, respectively; $P < 0.05$; Fig. 4A, left panel), whereas pawscraping, sniffing, watching and side-to-side were less frequent in H8 rabbits than H3 rabbits (0.3 vs 1.1%, 6.2 vs 8.4%, 7.2 vs 9.1% and 3.2 vs 9.2%, respectively; $P < 0.05$). In this same space and period, resting was more frequent on the pastures provided with a hideout (17.2 vs 5.8% in Y vs N, respectively; $P < 0.05$), while *Hopping* was less frequent (9.1 vs 12.4% in Y and N, respectively; $P < 0.05$; Fig. 4A, right panel).

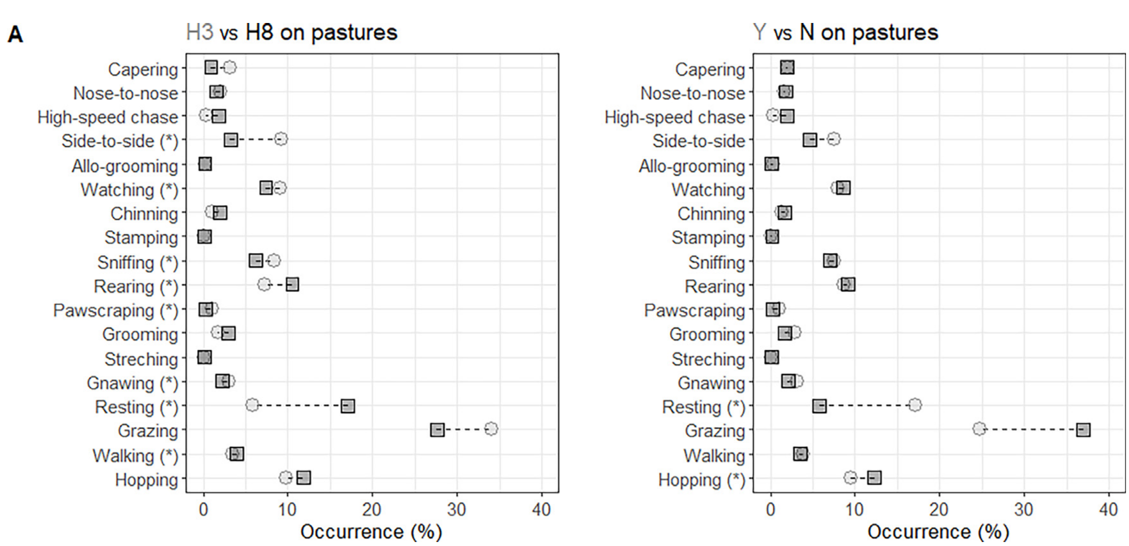

Fig. 4. Effect of access time (H3: 3 hours a day, or H8: 8 hours a day) and hideout presence (Y: with a hideout; N: no hideout: N) on rabbit behaviours (%) at 43, 60 and 74 days of age (**A**) outside on pastures and (**B**) inside the pens. An (*) means that the differences are statistically significant ($P < 0.05$).

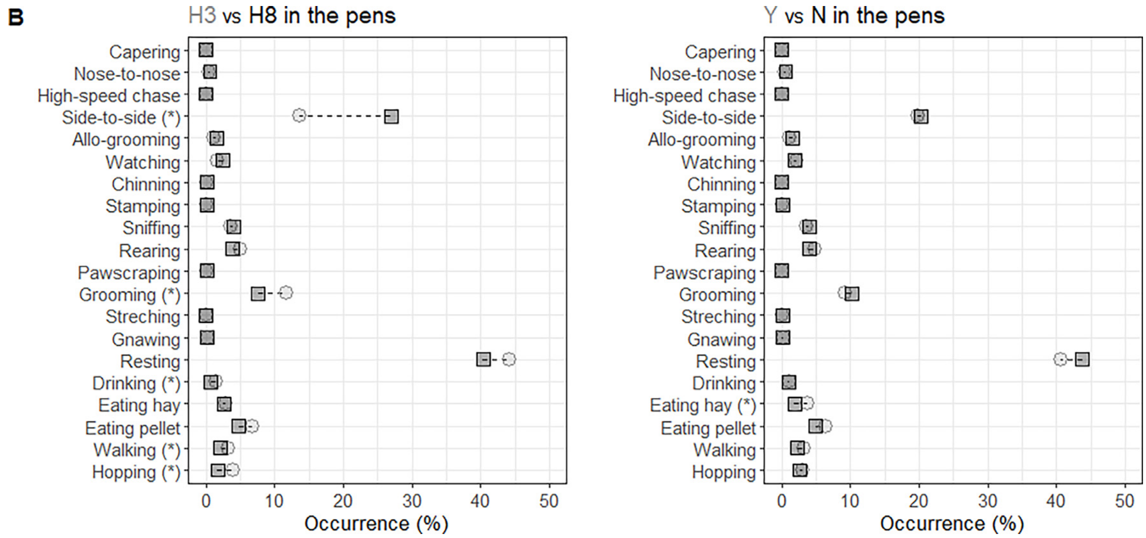

Fig. 4 (*continued*)

In the pens, in the morning and over all ages, rabbits in the H3 group were more frequently observed hopping, walking, drinking and grooming than rabbits in the H8 group (4.0 vs 1.7, 3.2 vs 2.1%, 1.4 vs 0.7% and 11.8%, respectively; $P < 0.05$; Fig. 4B, left panel). Side-to-side was more frequent in H8-group rabbits than H3-group rabbits (26.9 vs 13.6%, respectively; $P < 0.05$). Eating hay was more frequent in Y-group rabbits than N-group rabbits (3.7 vs 1.9%, respectively; $P < 0.05$).

On pastures, in the afternoon and over all ages for the H8 group only, rabbits were mostly observed grazing (on average, 28.2% of the observed behaviours; Supplementary Table S3). Resting was the most frequently expressed afternoon behaviour in the pens, independently of age, access time or hideout presence (on average, 49.3% of observations; Supplementary Table S4).

Description of rabbit behaviour under the hideout

Over all groups and ages, the most frequently expressed behaviours under the hideout were resting (34.7%), sniffing (27.2%) and grazing (15.3%) (data not shown). At day 56, H8 rabbits more frequently expressed grazing behaviour under the hideout than H3 rabbits (30.0 vs 0.0%, respectively; $P < 0.05$; Fig. 5). Resting under the hideouts was mostly expressed on hotter days (70.7% of occurrences at 26 °C recorded on day 56; Fig. 5 and Supplementary Fig. S4A).

Discussion

The aim of this study was to evaluate the effects of on-pasture access time and on-paddock hideout presence on growth, health, behaviour and corticosterone level (as a proxy of stress) in growing rabbits. No interaction between hideout presence and access time effects was observed except for herbage height at 77 days. That may be related to the low number of repetitions of the combination (two for each).

The results showed that pastures in which rabbits had longer access time had more areas of bare ground than when access time was shorter. However, there was no difference in the amount of on-ground biomass and, based on observed behaviours and corticosterone levels, limited access time to the pasture did not generate stress but frustration instead in the rabbits. However, rabbits given a shorter access time, including rabbits that did not have a

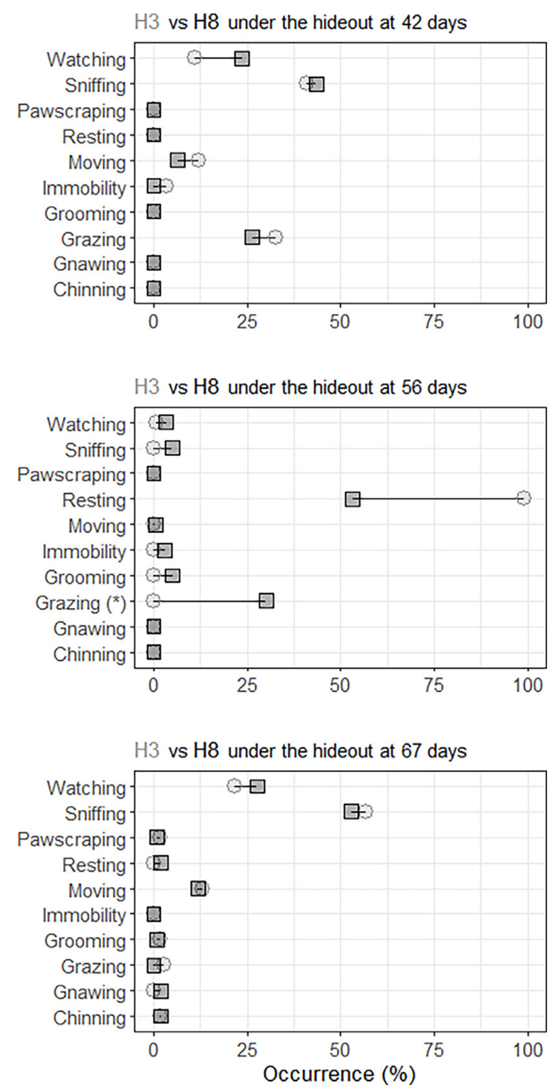

Fig. 5. Effect of access time (H3: 3 hours a day, or H8: 8 hours a day) and age (42, 56 or 67 days) on the rabbit behaviours (%) under the hideout. An (*) means that the differences are statistically significant ($P < 0.05$).

hideout, doubled their biomass intake rate and modified some of their behaviour patterns when outside by resting less, for example. Rabbits actively explored their living space and their use of the hideout was of short duration (they were not frequently observed under it).

Growth traits, health, and general behaviour of rabbits in the outdoor access system

The live weight of rabbits with restricted outdoor access time (on average, 2 187 g at day 67, H3 and H8 groups combined) was close to the live weight of similar-genotype rabbits (on average, 2 113 g at day 67) housed and reared in similar systems (the same mobile house placed on the same pasture) but with full-time outdoor access (Fetiveau et al., 2023). However, the mortality rate was higher in our study than in this previous study (18.7 vs 9.9%), due to an outbreak of epizootic rabbit enteropathy. The disease emerged in the present trial when rabbits were aged 55 days. About ten days before, the same disease emerged in caged rabbits housed in a building nearby. The animals (in cages and in the present trial) were managed by the same staff (no prophylactic measures were taken other than changing clothes and footwear). This situation supports the hypothesis that this health problem was not due to the system with outdoor access. Furthermore, although no clinical signs of coccidian parasitism were observed, the measured *Eimeria* sp. counts cannot rule out the hypothesis that our rabbits experienced subclinical coccidiosis in addition to epizootic rabbit enteropathy. Accordingly, the high mortality rate due to epizootic rabbit enteropathy may be amplified by a subclinical coccidiosis.

Biomass remains available on pastures until the end of the fattening period, whereas Fetiveau et al. (2021 and 2023) reported that all on-ground green biomass was entirely consumed when rabbits had full outdoor access (25 or 50 rabbits in a 23-m^2 pasture area and 24 rabbits in a 30 or 60 m^2 pasture area, respectively). This difference may be explained by restricting rabbit access to the paddock during the hours when rabbits usually graze the most (at dawn, at dusk and during the night; Mykytowycz and Rowley, 1958), together with the lower stocking density applied here. However, only two botanical species, *Hordeum murinum* and *Rumex crispus*, still remained on the pasture at the end of the fattening period. These results confirm that rabbits are selective eaters (Southern, 1940; Myers and Poole, 1959): we found appetence for some species such as *Lolium perenne*, *Trifolium repens* and *Crepis setosa*, and aversion for others such as *Hordeum murinum* and *Rumex crispus*. Hay intake was globally low during the whole fattening period, in line with Duprat and Goby (2016) and Fetiveau et al. (2023) who showed that rabbits eat little hay if pelleted feed and grass are available. The deprivation of herbage during the night (Mykytowycz and Rowley, 1958) could explain the higher pelleted feed consumption found in our study (115.1 g/day/rabbit) than in Fetiveau et al. (2023) in which rabbits had unlimited access to outdoor pasture (110.7 g/day/rabbit).

The spatial distribution of the rabbits reflected their circadian cycle since rabbits were more frequently observed outside on pastures than inside in the pens during the morning session, as previously shown by Fetiveau et al. (2021). In the pens, the rabbits did not frequently use the platforms and were mostly found under them (at least in the presence of humans). We contend that the area under the platforms mimics a shelter for the animals (Lombardi et al., 2007; Beja et al., 2007), making the rabbits feel safe in the presence of humans and the derived stimuli they impose (noise, movements, etc.). Moreover, Lang and Hoy (2011) showed that the number of rabbits climbing and staying on elevated platforms was significantly higher in darkness than in daylight since wild rabbits tend to stay under covered areas and in burrows during daytime (Kolb, 1986).

Effect of restricted access time

In accordance with our hypothesis, limiting pasture access proved to be an efficient strategy to prevent or postpone bare pasture ground. Pérez-Ramírez et al. (2008) showed that in dairy cows, the time spent grazing and pasture intake rate increased when pasture access time decreased (from 8 to 4 hours a day), which indicates a higher motivation for grazing. Here, grazing was always the dominant behaviour (on average, 30.9% of the observations), regardless of access-time conditions. Moreover, the rabbits with a shorter access time to pasture adjusted their daily herbage intake by increasing their grazing speed almost twofold over the whole growing period. This result suggests that rabbits are strongly motivated to graze and have the ability to adapt their grazing behaviour when they are aware of a constraint, although we cannot conclude more assertively without further information about the time budget for each behaviour. Future trials could benefit from combining both scan sampling and focal sampling (Altmann, 1973) to refine this analysis.

Pawscraping and sniffing were more frequently observed and resting was less frequently observed outside on pastures for rabbits given only 3 h access to the outdoors. This may be indicative of a drive to forage more (numerically higher), as further corroborated by the faster intake rate and a more active or even vigorous state of the rabbits when in the outdoor area, possibly induced by the rabbits adapting to restricted outdoor access time. Our results did not show an effect of access time on the behaviour of rabbits in the afternoon. However, it would be interesting to study whether rabbits with restricted access time to the pasture postpone their resting behaviour to a later time when they do not have access to the pasture.

Analysis of the time taken to return the rabbits to their pens did not reveal differences between H3 and H8 groups. Moreover, hair corticosterone levels were similar between groups, which means that both groups had the same level of stress. The absence of differences in time needed to return the rabbits to their pens may reflect a routinisation process where the experimenter's voice and physical presence inside the pastures accustomed them to the daily routine of time to leave the pastures. This routine would have become predictable for the rabbits and may therefore have prevented additional stress (Basset and Buchanan-Smith, 2007). However, the lack of positive (no outdoor access) and negative (full outdoor access) control groups in this trial limits our scope for further discussion on this point. The time taken for rabbits to exit the rabbit house was similar between the H3 and H8 groups. However, we observed behaviours linked to exploration and locomotion and frequently saw and heard (authors' personal observation) rabbit behaviours such as scratching against the hatches and stamping in the mornings just before opening the hatches, which can be interpreted as an arousal of activity. The results showed that the majority of the rabbits were gathered near the hatches when the experimenter was about to open it. We posit that, at this moment, both the spatial distribution and behaviours of the rabbits were indicative of the rabbits' anticipation of a positive event, i.e., gaining access to the outdoors and the opportunity to graze. Time of day, presence of the experimenter and past experiences may have acted as a sort of positive conditioning that was revealed through these indirect observations. Indeed, Anderson et al. (2015) showed that anticipatory behaviours in relation to a positive event are expressed as an increase in activity and spatial proximity to where the reward is presented. However, the variability in the time taken to free all the animals in the different pens could have induced inequity, which has yet to be proven (van Wolkenten et al., 2007), and/or frustration in the rabbits since a long waiting time induces frustration, which is an aversive state that results from non-reward, reduced reward or delayed reward in the presence of a history of reward (Amsel, 1992).

Effect of hideout presence

The rabbits tended to make little overall use of the hideouts. However, resting under the hideouts was mostly expressed on hotter days, in agreement with Thompson (1951) who showed that sunshine and hot temperatures increase resting behaviour in rabbits. This result might indicate that providing a hideout in the pastures could help the rabbits cope with heat stress, but we cannot confirm this conclusion since we did not measure the temperature under the hideouts. Rabbits tended to use the hideout more as a pass-through, without lingering in it. However, sniffing and gnawing along the outside rims of the hideouts were frequently observed (authors' observation) since the hideouts were made of wood, which rabbits commonly used for these two behaviours, as shown by Bozicovich et al. (2016). Moreover, rabbits were more frequently observed to be resting in pastures that had a hideout than in the environmentally unenriched pastures, suggesting that the animals felt more apt outside to express behaviours (resting here) that are usually more commonly observed indoors in pens.

Outside, the rabbits grazed the whole surface area of the pastures, even if they were more frequently found in the first 2.5 m closest to the hatches. The hideout provided (for a 3×10 m paddock) did not therefore affect the spatial distribution of the animals. However, it is reasonable to question whether the structural enrichment was appropriately adapted and in sufficient number for the paddock space and group size. Lombardi et al. (2007) showed that the preferred habitat type of rabbits in grasslands was shrubs that provide refuges and help escape predation, and that rabbit spatial distribution was related to the availability of refuges and not to the availability of food. In our study, rabbits were mostly observed near the rabbit house entrance hatch, which suggests that they felt that their refuge was the pen rather than the hideout. This could also be linked to the time of day that the observations were made. Moreno et al. (1996) showed that more rabbits ventured far from their burrow during the night, with up to 50% of them at an 18-m distance from the burrow, whereas 90% of them did not venture further than a 2-m distance during the day. Furthermore, the hideouts used were open-walled and relatively exposed, whereas studies have shown that rabbits prefer a closed, protective, burrow-type environment for hiding (Mykytowycz and Rowley, 1958; Kolb, 1986; Villafuerte and Moreno, 1997). It would be useful in further trials to study the behaviour and spatial distribution of rabbits that have access to pastures enriched with trees, bushes and scrub with a higher concealment potential.

Finally, rabbits that had access to a paddock equipped with a hideout consumed twofold less green biomass per hour than rabbits that had no structure enrichment. This suggests that providing a hideout or another kind of enrichment outside enables the animals to diversify their behavioural repertoire (such as resting).

Conclusion

Results obtained through this study showed that access time and hideout presence had no effect on rabbit growth and rabbit health but did influence rabbit behaviour. Enrichment of pastures with a hideout offers rabbits a place to rest outside. Further studies could address a better design of this enrichment and its effectiveness as a way to help rabbits cope with various types of stress (e.g., frightening noises, sight of a predator or heat stress). A shorter access time to pastures made it possible to slightly spare the grass resource and to extend the grass on offer for a little longer. Measures of hair corticosterone levels and time to get back into the rabbit house did not reveal any evidence of frustration in the rabbits, but we cannot confirm this conclusion since we did not have positive and negative control groups. Nevertheless, the excitement of the animals at the time of opening the hatch and the fact that the rabbits took little time to exit the rabbit house suggested that the rabbits experienced positive anticipation which, combined with the high expression of grazing behaviours observed, demonstrated that the rabbits were strongly motivated to graze outside. The overall faster biomass intake rate for shorter access time to pastures also suggests a strong motivation to graze, as well as an ability of the rabbits to adapt their behaviour in anticipation of a deprivation to come. Further studies are required to better characterise the determinants of rabbit motivation and foraging behaviour in relation to pasture structure and species composition and would constitute a step towards the wider goal of designing production systems with outdoor access that better meet rabbits' needs.

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2023.100724.

Ethics approval

Animals were handled in accordance with the recommendations of the European Union (2010) and French legislation on the protection of animals used for scientific purposes (EU Directive 2010/63/EU, Official Journal of the French Republic (Decree No. 2013-118)). All the protocols were approved by the Ethics Committee no 115 of the French Ministry of National Education, Higher Education and Research (approval number 16330-2018072716211212).

Data and model availability statement

None of the data has been deposited in an official repository. Access to the data can be made available upon request.

Author ORCIDS

M. Fetiveau: https://orcid.org/0000-0001-5374-8950
D. Savietto: https://orcid.org/0000-0002-1833-5832
L. Fortun-Lamothe: https://orcid.org/0000-0002-3300-8178
V. Fillon: https://orcid.org/0000-0003-3289-7417

Author contributions

M. Fetiveau: Conceptualisation, Methodology, Investigation, Formal analysis, Writing–Original Draft, Visualisation, Project administration.

D. Savietto: Methodology, Validation, Formal analysis, Writing–Review & Editing, Visualisation.

V. Fillon: Methodology, Validation, Writing–Review & Editing, Visualisation.

C. Bannelier: Investigation, Formal analysis, Writing–Review & Editing.

S. Pujol: Investigation, Resources.

L. Fortun-Lamothe: Conceptualisation, Methodology, Validation, Visualisation, Investigation, Writing-Review & Editing

Declaration of interest

The authors declare no conflict of interest of any sort.

Acknowledgments

The authors thank C. Trainini, M. Paccanelli, C. Lille-Larroucau, V. Helies, F. Benitez and F. Richard for handling daily care of the animals. We also give special thanks to all the rabbits we worked with.

Financial support statement

This study received financial support from INRAE under the SANBA metaprogram (grant for PANORAMA project, PArticipative desigN to enhance OutdooR Access of farM Animals; 2021–2024).

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