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ABSTRACT

Providing rabbits with an outdoor access allows them to express a large repertoire of their specific behaviours and addresses societal expectations concerning animal welfare in livestock systems. There is a need to provide knowledge on outdoor raised rabbits as, in Europe, almost all rabbits are raised in wired cages. The objective of this study was to describe the behaviours of rabbits living outdoors and the effect of genotype and pasture size. Focal sampling was used to score behaviours, and we tested the effects of pasture size and rabbit genotype on the expression of their specific behaviours. We divided 192 weaned rabbits into two experimental groups that differed in pasture size, *i.e.* a large pasture (**LP**) of 60 m^2 (n = 96, in 4 pens with their own outdoor access) and a small pasture (**SP**) of 30 m^2 (n = 96, in 4 pens with their own outdoor access). Each group contained rabbits of two genotypes, *i.e.* half ♂ 1001 × ♀ 1777 rabbits (**1001**) and half ♂ PS119 × ♀ 1777 rabbits (**PS119**). Rabbit behaviour was assessed for three 15-minutes periods (07:00–08:00 h, 14:00–15:00 h, and 19:00–20:00 h) when animals were aged 45, 59 and 71 days old by scoring behaviours from video recordings. The rabbits spent most of the time outside on the pastures than in the pens inside the building (56.9% *vs* 43.1% of the time, respectively). They expressed a large variety of species-specific behaviours, with grazing being predominant on the pastures (25.9% of observed time) and resting being predominant in the pens (34.2% of observed time). Results reflected the crepuscular nature of rabbits, as active behaviours were mainly displayed in the morning and in the evening. More time was spent hopping, grazing and watching in LP than SP pastures (on average, 2.5% *vs* 1.8%, 31.1% *vs* 24.6% and 9.9% *vs* 7.1%, respectively; $P < 0.05$). PS119 rabbits spent more time rearing and watching than 1001 rabbits (on average, 2.3% *vs* 1.1% and 9.6% *vs* 7.4%, respectively; $P < 0.05$), while 1001 rabbits spent more time grazing than PS119 rabbits (on average, 34.7% *vs* 22.1%, respectively; $P < 0.05$). This study finds that a larger pasture size promotes the expression of species-specific behaviours. Furthermore, patterns of some behaviours varied according to genotype. These results can be used to encourage farmers to provide an outdoor area to rabbits and to choose genotypes that are better adapted to outdoor conditions.

1. Introduction

In the EU, more than 90% of all meat rabbits live in wire cages within closed buildings (Szendrö et al., 2019) that restrict the expression of behaviours such as grazing and hopping, to the detriment of animal welfare (Lehmann, 1987). Nevertheless, alternative systems, although in minority, exist. For instance, in France, only 1% of organic meat rabbits have access to an outdoor area with at least 0.5 m^2 per animal (European Commission, 2020). Space is yet an important aspect of rabbit's life. In the wild, rabbits can travel more than 2000 m daily (Vastrade, 1987) and their home range can go up to 4 ha per individual (Coureaud et al., 2015). Space affects rabbit's behaviour because an increase in spatial availability increases locomotor activity (Jekkel et al., 2010; Dixon et al., 2010) and diversifies their behavioural repertoire (Fetiveau et al., 2021). Another component that can influence the expression of behaviours is genotype. Rabbits' genotype has mainly been studied regarding its effect on growth traits rather than on behavioural expression (Mugnai et al., 2014; Dalle Zotte et al., 2015). Nevertheless, Mugnai et al. (2008)

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showed that Leprino of Viterbo rabbits, characterized as a more robust breed, expressed more social behaviours than New Zealand White rabbits, characterized as a more productive breed (the most raised breed in the actual production system as well as its crossbreed with Californian rabbits), when both were pasture reared.

Behavioural studies can be used to indicate whether the animals' behavioural needs are being met (Dawkins, 2004). Furthermore, these studies also deal with animal's adaptation to environments in which they were put by humans (Broom, 1986; Fraser et al., 1997). Thus, they serve as a basis for animal welfare assessment. The living environment in which farmed animals are kept includes all the non-genetic factors that can influence responses and interact with the animals' genotype (King, 2006). Better meeting the needs of animals to improve their welfare can be achieved by adapting the living environment to both the physiological and behavioural needs of animals, by choosing individuals that are already adapted (or pre-disposed to adapt better) to their environment, or by considering environment–genotype interactions (Mirkena et al., 2010). To contribute to the design of welfare-friendly systems with access to outdoor areas, the main objective of the current study was to describe the behaviours of rabbits living outdoors and the effect of genotype and the pasture size. Variation of behaviour with time of day and rabbit age was also studied. The present work compared rabbits from two genotypes differing in selection history. We hypothesised that (i) a larger pasture area would enable rabbits to spend more time grazing than a smaller pasture area, and that (ii) genotype may have an influence on the expression of specific behaviours such as social interactions and maintenance.

2. Material and methods

2.1. Animals and housing

A total of 192 rabbits (50% males and 50% females) were reared for 42 days starting from weaning (at 31 days of age; 25th March 2021) to 72 days of age (5th May 2021). Rabbits were housed in a 30 m^2 building placed on a pasture and equipped with eight 2 m^2 roofless pens. Each pen was equipped with a hayrack (W × L × H: 24 × 41 × 48 cm) placed on the opposite side to the feeder. The longitudinal walls of the building had 4 hatches (W × H: 39 × 42 cm) cut out to allow access to the pasture in front of each pen. The building thus counted 8 pens inside, each pen giving access to an outside pasture (n = 8 pastures; See Supplementary Fig. S1). No artificial lighting was provided in the building except for infrared light from an infrared lamp (175 W) placed above the pens (at 70 cm above ground level) between days 31 and 42 from 23:00 h to 06:00 h to prevent thermal stress caused by temperatures below 15 °C during the night. The outdoor area was protected from predators by a three-wire electric fence. The pastures were enclosed by a sweet-chestnut (Castanea sativa) fence (H: 1.0 m). The pastures were in a meadow sown in 2016 with pure fescue (*Festuca arundinacea*). The experiment took place in April 2021 and the grassland was composed of various herbaceous plants (*Lolium perenne*, *Trifolium repens*, *Crepis setosa* and *Dactylis glomerata*).

Half of the rabbits (n = 96) were crossbred Californian 1001 × New-Zealand 1777 (both INRAE genetic types selected on post-weaning growth rate; **1001**). The other half (n = 96) were PS119 × New-Zealand 1777 (semen from a commercial genetic type selected for robustness and carcass weight; https://hypharm.fr/en/products/male-ps-119/ ; Hypharm, 49450 Sèvremoine; **PS119**) (see Supplementary Fig. S2). At weaning, rabbits of both sexes and both genotypes were distributed into two experimental groups differing in pasture surface area, *i.e.*, 60 m^2 (W × L: 6 × 10 m; Large pasture: LP) or 30 m^2 (W × L: 3 × 10 m; Small pasture: SP). Each group, housed in a pen having access to one pasture, contained 24 rabbits (*i.e.*, 12 '1001′ and 12 'PS119′; half males and half females). The rabbits were allowed continuous access to the pasture from days 37–73. Throughout the experiment, the rabbits were fed *ad libitum* with a pelleted diet without anti-coccidian (STABI-FIBRE, Terrya, Rignac, France; 15.2 MJ of gross energy per kg DM, 15.0% CP, 3.0% fat, 41.2% NDF, 20.8% ADF and 6.4% ADL on a DM basis) plus sainfoin (*Onobrychis viciifolia*) hay (15.6 MJ of gross energy per kg DM, 4.4% CP, 56.6% NDF, 43.1% ADF and 10.2% ADL on a raw basis).

2.2. Behavioural observation

For rabbits, animal marking techniques developed and used since the mid-20th century have been disking, tattooing and dyeing (Thompson and Amour, 1954; Rowley, 1956). However, the use of plastic discs attached to the rabbit's ear has disadvantages, as several of the tagged rabbits lose their disk and many others show suppuration between the disk and washer (Southern, 1940). Ear tattoos are hard to spot from a distance and the ears can get damaged by fighting (Rowley, 1956). Dyeing, using a dye applied either on the rabbit's head, forequarters, girth, hindquarters or back, is effective in terms of visibility, but once dye-marked, the rabbits have to be separated to prevent colour transference and allogrooming (Rowley, 1956). In the present study, we used coloured cotton cloaks inspired from Fanatico et al. (2016) and Ferreira et al. (2019) which enabled us to individually identify the exact same animals over different observation periods and days.

The behaviour of the animals was assessed during 15 min × 3-observation periods using the focal sampling method (Altmann, 1973) with continuous recording when the rabbits were 45, 59 and 71 days old. Cameras (GoPro, Hero 7) were installed to capture the range area of each pen and pasture (one fixed camera per pen and per pasture placed at 1 m height, see Supplementary Fig. S1). Video recordings were later decoded by a single observer. A resting pause of 10 min was taken every 2 videos to prevent visual fatigue and drift. Observations were made in the morning (15 min between 07:00 h and 08:00 h, just after sunrise), in the afternoon (15 min between 14:00 h and 15:00 h) and in the early evening (15 min between 19:00 h and 20:00 h, just before sunset). Ten rabbits per pen were chosen randomly for individual observation (50% 1001 × 1777 and 50% PS119 × 1777). The same ten rabbits per pen were observed at all ages with the help of handmade coloured cotton cloak with elastic straps (L × W: 16 × 13 cm; Supplementary Fig. S3). We showed that the cloaks did not disturb the rabbits. Each rabbit within the same genotype was equipped with either a yellow, blue, purple, red or pink cloak (Supplementary Fig. S4). The rabbits were dressed an hour before the beginning of the morning observation session to habituate them to the cloaks. Cloaks were removed after the evening observation session (*i.e.* they spent the whole day dressed up). These handmade cloaks were pre-tested two months before the experiment to make sure they did not disturb the rabbits and alter their behaviour. We compared the behaviours of rabbits wearing a cloak to the behaviour of rabbits that were not fitted with a cloak. To do this, we used nineteen percent of the total number of videos. The videos were chosen randomly, at different ages, periods of the day and place of observation. Four rabbits (two with a cloak and two without a cloak) were followed for 15 min and their behaviours were recorded. Video recordings were analyzed using Boris software v.7.9.24 (Friard and Gamba, 2016). We were able to collect data from 95% of the dressed rabbits. The following behaviours described by Gunn and Morton (1995) and Coda et al. (2020) were recorded (see Supplementary Table S1): moving (*Hopping* and *Walking*), maintenance (*Grazing*, *Eating pellets*, *Eating hay*, *Drinking*, *Resting*, *Gnawing*), comfort (*Stretching*, *Yawning*, *Grooming*), exploration and alertness (*Pawscraping*, *Rearing*, *Sniffing*, *Stamping*, *Chinning*, *Watching*), and interaction (between two rabbits or more: *Allogrooming*, *Side-to-side*, *High-speed chase*, *Nose-to-nose*) and *Capering*.

2.3. Statistical analyses

All statistical analyses were performed using R statistical software version 4.2.1 (R CORE TEAM, 2020). The package used for analysis was lme4 and p values were extracted with Laplace approximation. To estimate the means, we used the R package emmeans and the Tukey method to adjust the p-value estimates for multiple tests.

The proportions in the data correspond to the time the observed rabbits spent performing a specific behaviour over the total time of observations for each location (pens or pastures).

Data was not normally distributed. It followed a negative binomial distribution confirmed by the difference in μ and σ and the over-dispersion of σ (evaluated with a chi-squared test). Data was then analyzed by fitting negative binomial GLMMs as follows:

$$glmer.nb(y \sim axb + c + d + (1|e));$$

where *a* is pasture size (2 levels: SP and LP) and *b* is genotype (2 levels: 1001 and PS119), both modelled as fixed effects (with their interaction used in the model), *c* is rabbit age (3 levels: 45, 69, and 71 days) and *d* is period of the day (3 levels: morning, afternoon, and early evening), set as co-variables. Finally, *e* was introduced into the model as a random effect associated with the rabbit observed (n = the same 80 rabbits at different ages observed in total) in a specific observation site (pens or pastures). For each variable, we computed the compound symmetry covariance structure of the variance-covariance matrix of errors. Statistical differences were declared at an alpha value of 0.05.

To test if fitting animals with a cloak changed their behaviour, data was analyzed by fitting negative binomial GLMMs with the rabbit's ID (2 levels: with or without a cloak) as main effect, rabbit age (3 levels: 45, 69 and 71 days) and period of the day (3 levels: morning, afternoon, and early evening) set as covariables and the pen as random effect.

Descriptive data was obtained from the same ten selected rabbits per pen (*i.e.*, 80 rabbits in total).

3. Results

The results showed no effect ($P > 0.05$) of the cloak on rabbit behaviour (see Supplementary Fig. S5).

3.1. Descriptive overview of rabbit behaviour in a pen system with access to pasture

The observed rabbits spent 56.9% of the time outside on the pastures and 43.1% of the time in the pens. On the pastures, *Grazing* and *Resting* were the predominant behaviours and accounted for 25.9% and 21.2% of observed time, respectively (Fig. 1. A). In the pens, *Resting* and *Side-to-Side* were the predominant behaviours and accounted for 34.2% and 30.4% of observed time, respectively (Fig. 1. B).

3.2. Period-of-the-day effects on behaviour

The rabbits spent more time outside on the pastures than in the pens in the morning and in the evening (on average, 64.9% *vs* 35.1% and 72.6% *vs* 27.4% of the time, respectively), but in the afternoon they spent less of their time on the pastures (35.9%) than in the pens (64.1%); descriptive statistics only.

On pastures (Fig. 2. A), rabbits spent, on average, 4.9% of the time *Hopping* in the morning but significantly less time *Hopping* in the evening (2.9%) and in the afternoon (1.9%) ($P < 0.05$). Percentage of time spent *Resting* and *Side-to-Side* was significantly higher ($P < 0.05$) in the afternoon (56.4% and 34.7%, respectively) than in the morning (26.3% and 17.2%, respectively) and in the evening (29.5% and 13.6%, respectively). Percentage of time spent *Grooming* and *Sniffing* was significantly lower ($P < 0.05$) in the afternoon (7.4% and 1.7%, respectively) than in the morning (20.8% and 3.4%, respectively) and in the evening (23.2% and 3.5%, respectively).

In the pens (Fig. 2. B), rabbits spent more time *Watching* in the morning and in the evening compared to the afternoon (on average, 9.3% and 11.0% *vs* 4.4%, respectively; $P < 0.05$) and more time *Sniffing* in the morning compared to the evening and the afternoon (on average, 6.5% *vs* 2.5% *vs* 1.6%, respectively; $P < 0.05$). Rabbits spent significantly more time *Resting* and *Side-to-Side* in the afternoon than in the morning (on average, 48.7% *vs* 30.5% and 38.7% *vs* 28.3%, respectively; $P < 0.05$), but without differences between afternoon and evening or between morning and evening.

3.3. Age effects on behaviour

At 45 days of age, rabbits spent more time in the pens than on the pastures (on average, 51.7% *vs* 48.3% of the time, respectively). At 59 and 71 days of age, rabbits spent more time on the pastures than in the pens (on average, 62.7% *vs* 37.3% and 58.9% *vs* 41.1% of the time, respectively); descriptive statistics only.

On pastures (Fig. 3. A), rabbits spent more time *Grazing* at age 45 and 59 days than at age 71 days (on average, 46.2% and 41.8% *vs* 18.2%, respectively; $P < 0.05$) and more time *Hopping* at age 45 than age 71 days and age 59 days (on average, 5.1% *vs* 3.4% *vs* 2.6%, respectively; $P < 0.05$). Rabbits spent less time *Resting* at age 45 days than at age 59 days and 71 days (on average, 24.4% *vs* 45.4% and 39.8%, respectively; $P < 0.05$). The rabbits also spent less time *Rearing* at age 45 days than at age 71 days (on average, 1.2% *vs* 2.0%, respectively; $P < 0.05$) and more time *Watching* at age 71 days than at age 45 days and 59 days (on average, 17.6% *vs* 7.2% and 7.4%, respectively; $P < 0.05$).

In the pens (Fig. 3. B), rabbits spent significantly more time *Eating hay* and *Drinking* at age 71 days than at age 45 days and 59 days (on average, 15.8% *vs* 2.2% and 3.6% and 10.5% *vs* 2.8% and 5.6%, respectively; $P < 0.05$). Moreover, rabbits spent significantly more time *Sniffing* and *Watching* at age 71 days than age 45 days (on average, 3.5% *vs* 1.4% and 12.6% *vs* 3.7%, respectively; $P < 0.05$). In addition, rabbits spent significantly more time *Allogrooming* at age 45 days than at age 71 days (on average, 3.2% *vs* 1.3%, respectively; $P < 0.05$).

3.4. Pasture-size and genotype effects on behaviour

PS119 rabbits spent more time on pastures than 1001 rabbits (on average, 61.2% *vs* 52.8% of the observed time, respectively). There was no pasture-size effect on the time rabbits (both genotypes) spent outside (on average, 49.5% on SP and 50.5% on LP); descriptive statistics only.

On pastures (Table 1), a significant interaction between pasture size and genotype was found for *Gnawing and Sniffing* ($P < 0.05$). More time *Gnawing* was spent for PS119 rabbits than 1001 rabbits in SP (on average, 2.6% *vs* 0.6%, respectively; $P < 0.05$) whereas the two genotypes spent a similar amount of time *Gnawing* in LP (0.5% *vs* 0.8%, respectively). More time *Sniffing* was spent for 1001 rabbits than PS119 rabbits in LP (on average, 4.0% *vs* 2.4%, respectively; $P < 0.01$) whereas the two genotypes spent a similar amount of time *Sniffing* in SP (on average, 2.9% *vs* 2.7% for 1001 *vs* PS119 rabbits). Rabbits spent significantly more time *Hopping*, *Grazing* and *Watching* in LP than SP (on average, 2.5% *vs* 1.8%, 31.1% *vs* 24.6% and 9.9% *vs* 7.1%, respectively; $P < 0.05$) but significantly less time *Side-to-side* in LP than SP (on average, 16.2% *vs* 25.3%, respectively; $P < 0.001$). PS119 rabbits spent more time *Rearing* and *Watching* than 1001 rabbits (on average, 2.3% *vs* 1.1%, and 9.6% *vs* 7.4%, respectively; $P < 0.05$) and significantly less time *Grazing* than 1001 rabbits (on average, 34.7% *vs* 22.1% for 1001 *vs* PS119 rabbits; $P < 0.001$).

In the pens (Table 2), the effect of pasture size × genotype interaction was significant for *Eating hay*, *Drinking*, *Chinning* and *Allogrooming* ($P < 0.05$). PS119 rabbits spent more time *Eating hay* in SP than LP (on average, 10.9% *vs* 2.0%, respectively; $P < 0.05$) while 1001 rabbits spent less time *Eating hay* in SP than in LP (and 1.6% *vs* 6.0%, respectively; $P < 0.05$). PS119 rabbits spent more time *Drinking* than 1001 rabbits in LP (on average, 9.9% *vs* 3.6%, respectively; $P < 0.05$) whereas there was no difference in SP. PS119 rabbits spent more time *Chinning* and *Allogrooming* in LP than in SP (on average, 1.9% *vs* 0.1% and 2.8% *vs* 0.6%, respectively; $P < 0.05$) whereas 1001 rabbits showed no between-pasture-size difference. Rabbits spent more time *Grooming* in LP than in SP (on average, 15.2% *vs* 9.2%, respectively; $P < 0.01$). 1001 rabbits

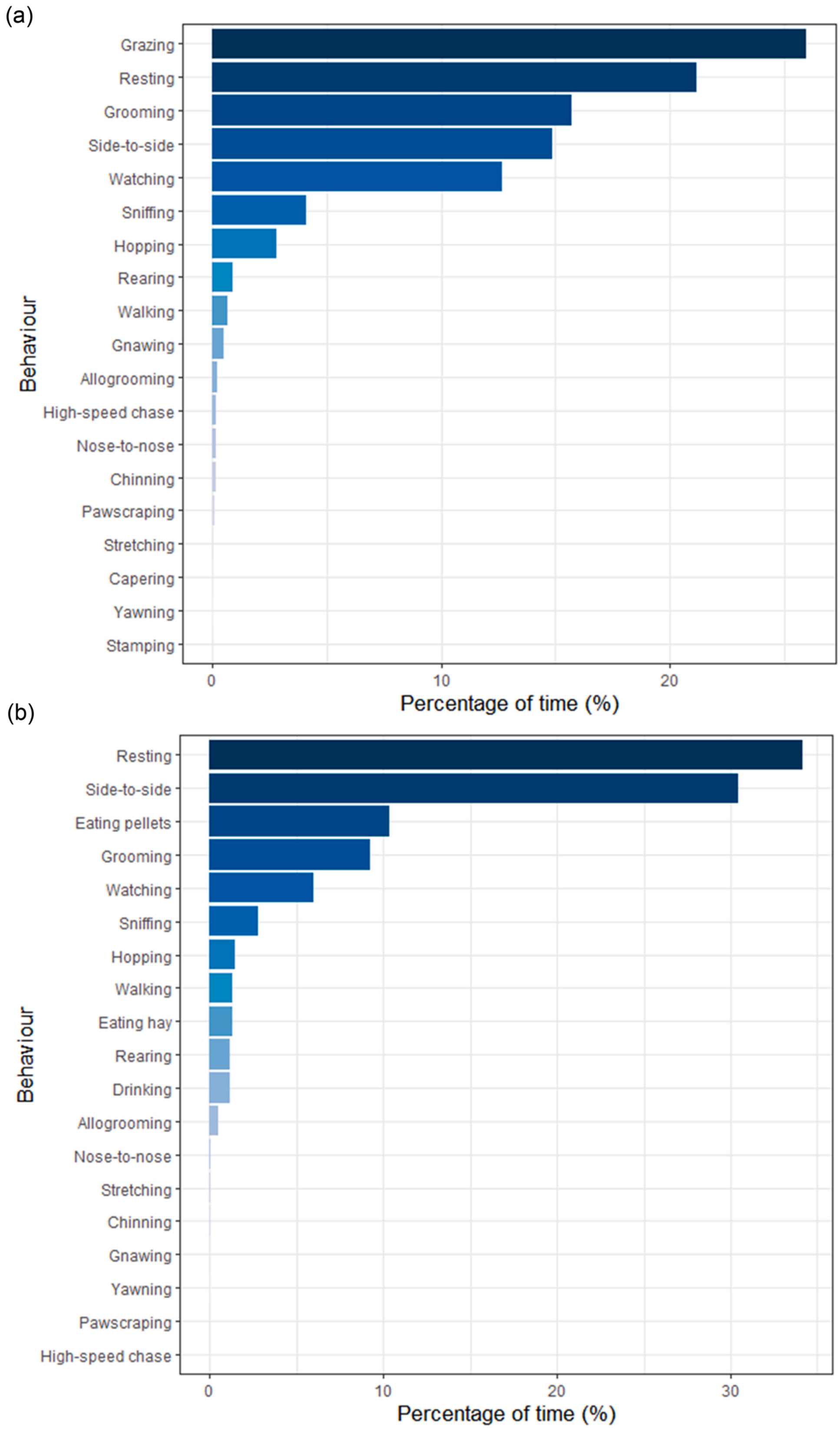

Fig. 1. A. Mean percentage (%) of observed time in which rabbits expressed specific behaviours outside on the pastures. B. Mean percentage (%) of observed time in which rabbits expressed specific behaviours inside in the pens.

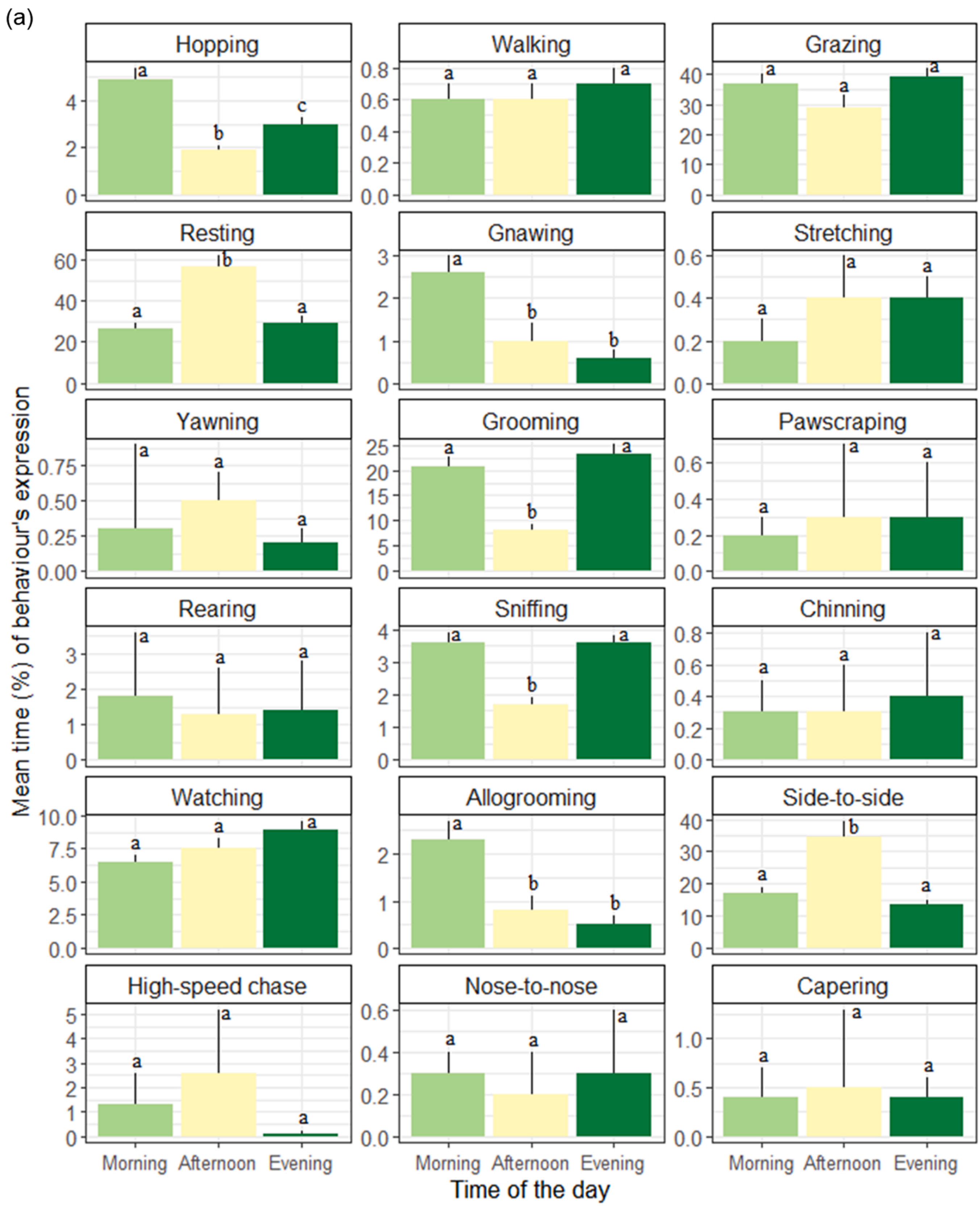

Fig. 2. A. Effect of time of the day (morning: light green, afternoon: yellow, evening: dark green) on the expression of rabbits' specific behaviours (expressed as percentage of total observation time) on the pastures. For each behaviour, bars with different letters (a,b,c) differ significantly at $P < 0.05$. The black lines represent the standard error. B. Effect of time of the day (morning: light green, afternoon: yellow, evening: dark green) on the expression of rabbits' specific behaviours (expressed as percentage of total observation time) in the pens. For each behaviour, bars with different letters (a,b,c) differ significantly at $P < 0.05$. The black lines represent the standard error.

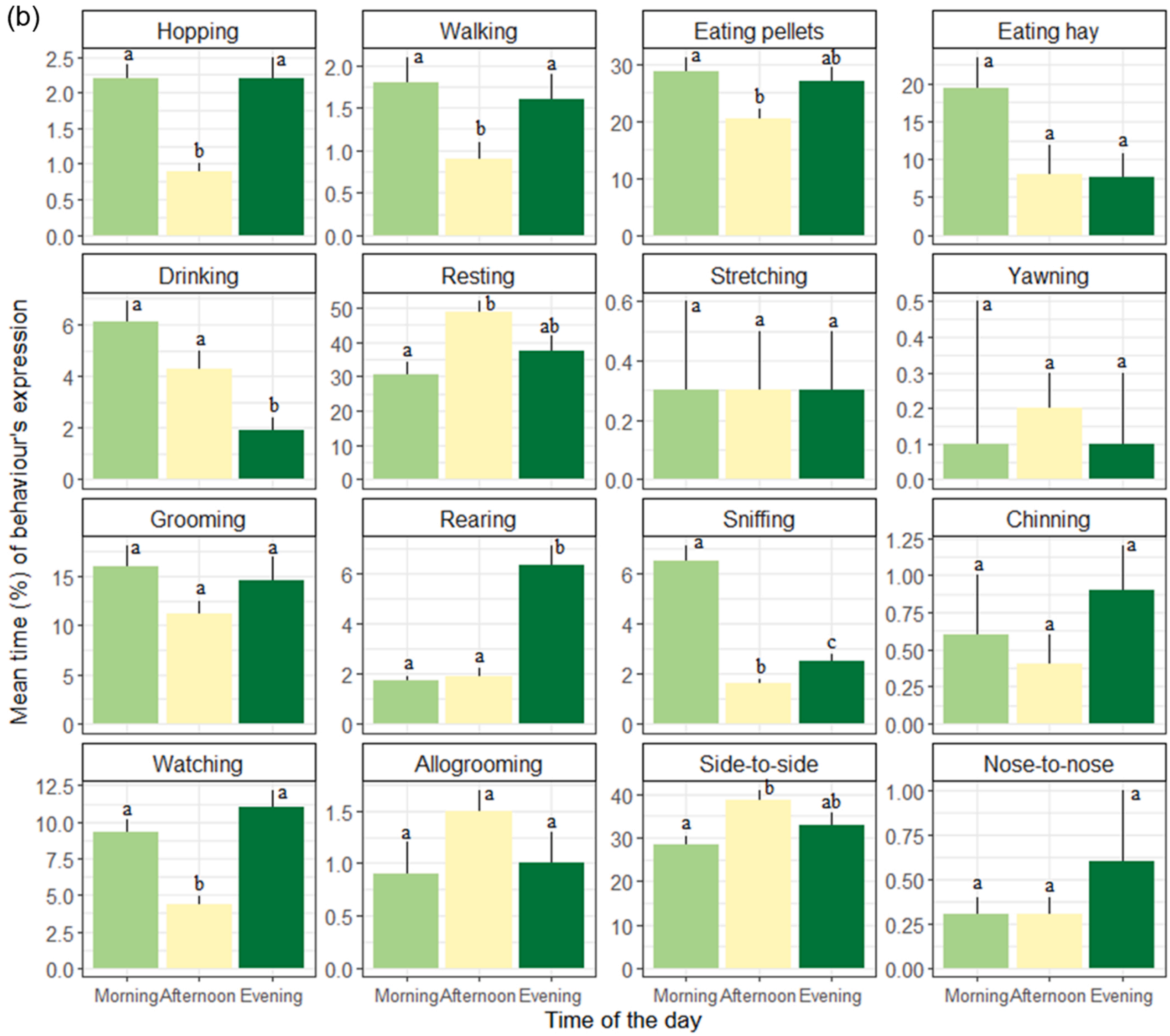

Fig. 2. (*continued*).

spent more time *Grooming* and *Sniffing* than PS119 rabbits (on average, 14.3% *vs* 9.8% and 3.8% *vs* 2.4%, respectively; $P < 0.05$) but less time *Rearing* than PS119 rabbits (on average, 1.7% *vs* 2.4%, respectively, $P < 0.05$).

4. Discussion

Our results showed that rabbit time budgets are dependent on (1) environment (longer time *Grazing* and *Resting* on pastures compared to *Resting* in the pens), (2) size of the grazing area (more time was spent *Grazing* in the 60 m^2 than the 30 m^2 pastures), and (3) rabbit genotype (PS119 rabbits spent more time *Rearing* and *Watching* and less time *Grazing* than 1001 rabbits on the pastures).

Rabbits spent the majority of their time outside on pastures, grazing. This corroborates observations by Prebble et al. (2015) who showed that rabbits spent between 30% and 70% of their time outside of their burrows grazing, with time spent grazing varying between 2.5 and 6.5 h a day. Our findings also fit well with Mykytowycz and Rowley (1958) who showed that wild rabbits spent an average of 47.2% of the observed time (12 h in their study) budget feeding. After grazing, the behaviour with the second longest duration on pastures was resting. This is again consistent with Mykytowycz and Rowley (1958) who showed that resting was the second-longest time budget behaviour. In the pens, rabbits spent more time resting close together than outside on pastures. This suggests that they used the pens as refuges where they displayed inactivity-related behaviours, as shown by Kolb (1986) and Postollec et al. (2008). The limited space available in the pens (2 m^2) may also explain the large amount of time rabbits spent side-to-side. The percentage of rabbit time budget spent expressing alertness behaviours such as watching, rearing and stamping was low both on pastures (on average, 12%, 2% and 0%, respectively) and in pens (on average, 6%, 2% and 0%, respectively). Vigilance is described as an anti-predator behaviour (Elgar, 1989) that enables rabbits to detect predators early and communicate the danger to other rabbits. Monclús et al. (2006) showed that young rabbits (under 1 year old) displayed less vigilance than adult rabbits (above one year old) and suggested that this was because vigilance inhibits foraging and the associated feed intake which may be more important for fitness in younger rabbits with higher growth than older rabbits. The same ecological principle may apply to our growing rabbits.

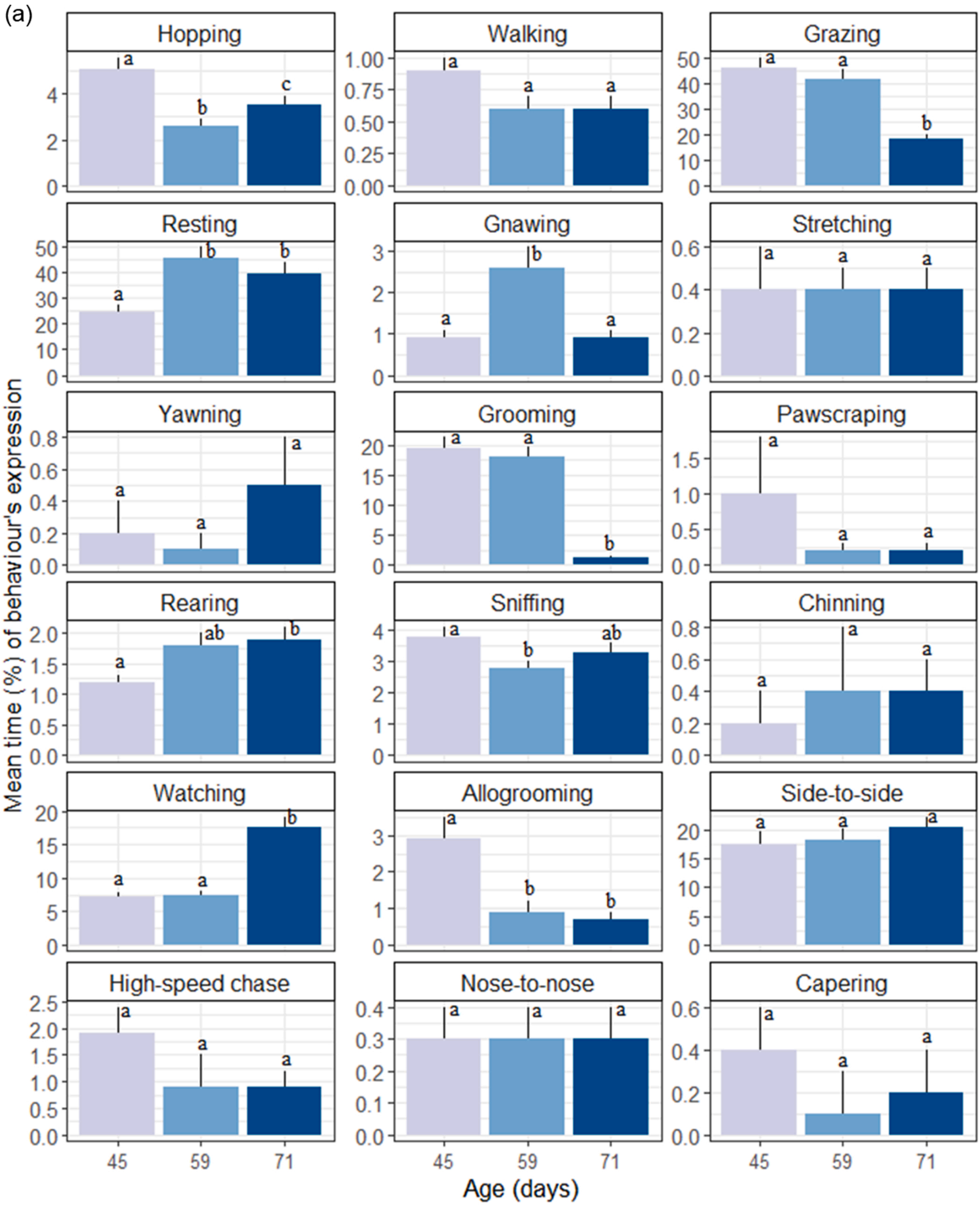

Fig. 3. A. Effect of age (45: grey, 59: light blue, and 71 days old: dark blue) on the expression of rabbits' specific behaviours (expressed as percentage of total observation time) on the pastures. For each behaviour, bars with different letters (a,b,c) differ significantly at $P < 0.05$. Black lines represent the standard error. B. Effect of age (45: grey, 59: light blue, and 71 days old: dark blue) on expression of rabbits' specific behaviours (expressed as percentage of total observation time) in the pens. For each behaviour, bars with different letters (a,b,c) differ significantly at $P < 0.05$. Black lines represent the standard error.

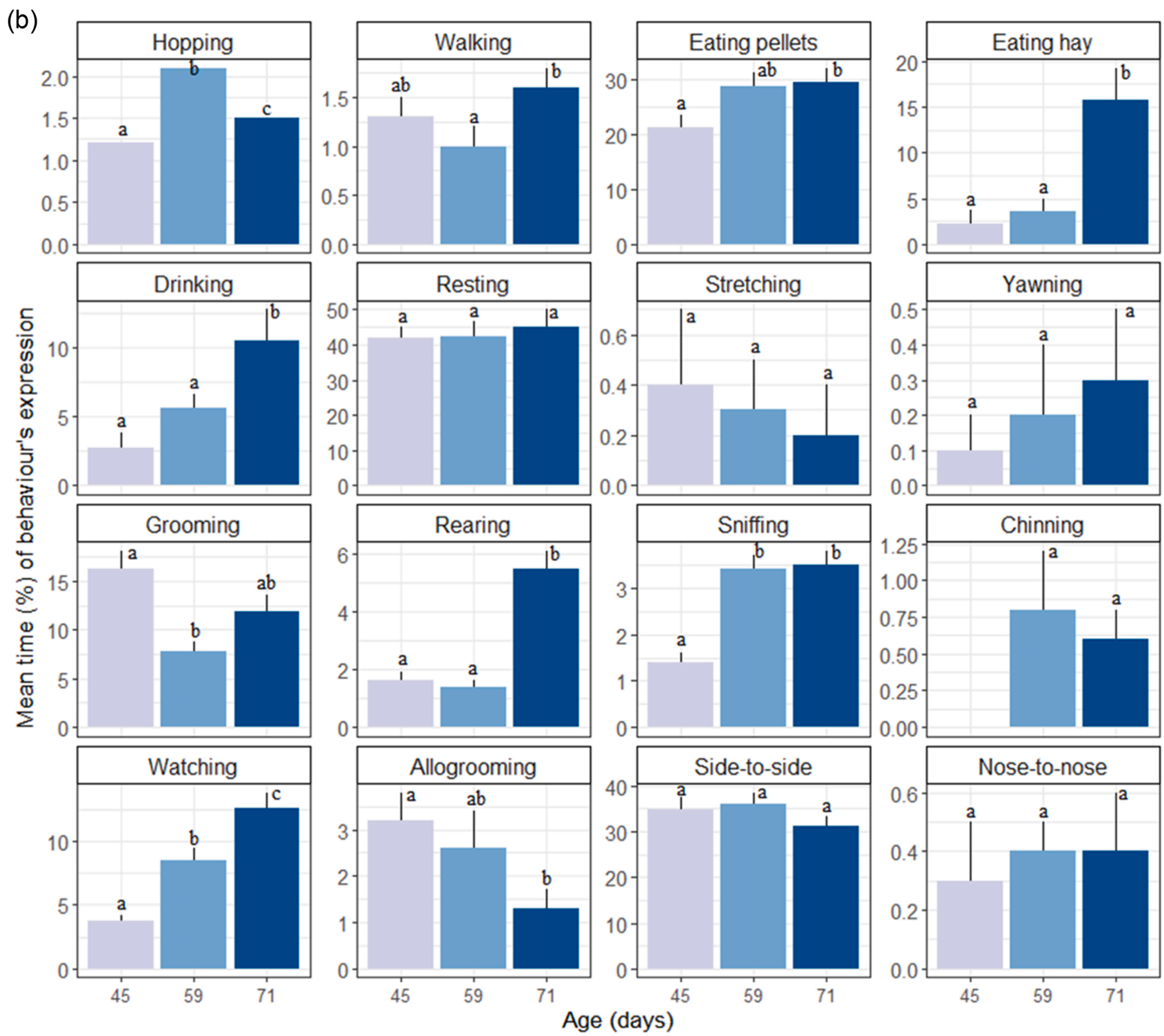

Fig. 3. (*continued*).

Rabbits spent more time on the pastures in the morning and in the evening, where they spent more time on locomotor behaviours, such as hopping, and comfort behaviours such as grooming, than in the afternoon. In the afternoon, they spent more time performing maintenance behaviours, such as resting, than in the morning and evening. This supports findings by Mykytowycz and Rowley (1958) and Podberscek et al. (1991) who showed that rabbits, like other crepuscular animals, were mainly inactive between 10h00 and 14h00 and most active in dark hours.

Rabbits spent more time grazing and less time resting on the pastures at age 45 and 59 days than at age 71 days. Fetiveau et al. (2023) showed, on the same trial, that on-pasture biomass (grass and legumes) was, on average with all pastures size combined, 16 times more abundant when the rabbits were aged 35 days than 73 days and 4.4 times more abundant when the rabbits were aged 59 days than 73 days. The shortage of available biomass on the pastures would then have limited the rabbits' ability and opportunity to graze, and led them to change the time allocated to each behaviour (Mykytowycz and Rowley, 1958).

Grazing is often carried out at the same time as a locomotory behaviour such as walking or hopping and occasionally at the same time as behaviours linked to vigilance, such as rearing and watching. Southern (1940) asserted that rabbits essentially have three different kinds of feeding behaviour, one of which was qualified as "normal feeding" characterized by true cropping carried out as a slow movement punctuated by raising the head in an alert posture at regular intervals. Here, we observed this "normal feeding" behaviour. The two other categories of feeding behaviour, *i.e.* "voracious feeding" (which often occurs before a storm with the head kept down the whole time) and "casual feeding" (in which the animal interrupts its basking to nibble idly at various plants and grasses), were not observed in the present study. Moreover, with larger space available (the 60-m^2 pastures) and, consequently, a higher biomass offered, the rabbits spent more time hopping, grazing and watching on the pastures. The observed difference in the expression of hopping between 60-m^2 and 30-m^2 pastures was however minor (2,5% and 1,8%, respectively) and the effect must be interpreted with care.

On pastures, PS119 rabbits spent more time expressing rearing and watching than 1001 rabbits. It thus seems that PS119 rabbits interacted for longer time with their environment, which could indicate that they are either more active or more alert than 1001 rabbits. In making this

Table 1
Mean (± SE) expression of specific rabbit behaviours (expressed as percentage of observed time) in the pastures according to pasture size (30 m^2: SP and 60 m^2: LP) and rabbit genotype (PS119 and 1001).

Genotype (G)	PS119		1001		P-value		
Pasture size (S)	LP	SP	LP	SP	S	G	S × G
Hopping (%)	2.4^{a} ± 0.2	1.9^{ab} ± 0.2	2.6^{a} ± 0.2	1.6^{b} ± 0.2	**< 0.001**	0.70	0.31
Walking (%)	0.7 ± 0.2	0.7 ± 0.2	0.6 ± 0.2	0.8 ± 0.2	0.56	0.85	0.47
Grazing (%)	24.4^{ab} ± 2.3	19.9^{a} ± 2.2	39.7^{c} ± 3.7	30.3^{bc} ± 3.0	**< 0.05**	**< 0.001**	0.71
Resting (%)	31.8 ± 3.5	36.1 ± 3.9	30.3 ± 4.1	30.0 ± 3.6	0.57	0.29	0.56
Gnawing (%)	0.5^{a} ± 0.3	2.6^{b} ± 0.6	0.8^{ac} ± 0.3	0.6^{c} ± 0.2	0.45	**< 0.05**	**< 0.05**
Stretching (%)	0.3 ± 0.8	0.3 ± 0.2	0.4 ± 0.2	0.5 ± 0.2	0.81	0.50	0.83
Yawning (%)	0.3 ± 0.4	1.4 ± 1.6	0.2 ± 0.3	0.3 ± 0.3	0.13	0.18	0.55
Grooming (%)	20.1 ± 2.2	17.2 ± 1.9	17.1 ± 1.9	15.7 ± 1.9	0.27	0.26	0.76
Pawscraping (%)	0.5 ± 0.6	0.3 ± 0.3	0.4 ± 0.3	0.3 ± 0.3	0.67	0.97	0.75
Rearing (%)	2.4^{a} ± 0.3	2.3^{a} ± 0.4	1.2^{b} ± 0.2	1.0^{b} ± 0.2	0.70	**< 0.001**	0.79
Sniffing (%)	2.4^{a} ± 0.3	2.7^{a} ± 0.3	4.0^{b} ± 0.4	2.9^{ab} ± 0.3	0.23	**< 0.01**	**< 0.05**
Chinning (%)	0.5 ± 0.5	1.1 ± 1.2	0.2 ± 0.3	0.3 ± 0.4	0.39	0.21	0.69
Watching (%)	10.6^{a} ± 1.2	8.7^{ab} ± 1.0	9.4^{a} ± 1.1	5.9^{b} ± 0.7	**< 0.01**	**< 0.05**	0.28
Allogrooming (%)	1.2 ± 0.3	1.5 ± 0.4	0.6 ± 0.4	1.5 ± 0.4	0.25	0.73	0.29
Side-to-side (%)	16.7^{a} ± 1.7	25.4^{b} ± 2.9	15.6^{a} ± 1.8	25.2^{b} ± 3.1	**< 0.001**	0.72	0.80
High-speed chase (%)	0.7 ± 0.5	0.5 ± 0.4	0.2 ± 0.2	0.4 ± 0.3	0.83	0.25	0.44
Nose-to-nose (%)	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.80	0.78	0.71
Capering (%)	0.3 ± 0.3	0.5 ± 0.5	0.2 ± 0.3	0.3 ± 0.3	0.68	0.84	0.74

a-c Means with different letters (a,b,c) in the same row differ significantly at an alpha value of 0.05

Table 2
Mean (± SE) expression of specific rabbit behaviours (expressed as percentage of observed time) in the pens according to pasture size (30 m^2: SP and 60 m^2: LP) and genotype (PS119 and 1001).

Genotype (G)	PS119		1001		P-Values		
Pasture size (S)	LP	SP	LP	SP	S	G	S × G
Hopping (%)	1.5^{ab} ± 0.2	1.3^{ab} ± 0.2	2.0^{a} ± 0.3	1.2^{b} ± 0.2	**< 0.05**	0.36	0.24
Walking (%)	1.3 ± 0.4	1.8 ± 0.5	1.3 ± 0.3	1.6 ± 0.4	0.38	0.82	0.89
Eating pellets (%)	28.5 ± 2.9	27.4 ± 2.8	24.6 ± 2.5	27.0 ± 3.2	0.83	0.41	0.54
Eating hay (%)	2.0^{ac} ± 1.0	10.9^{b} ± 4.6	6.0^{c} ± 2.4	1.6^{a} ± 0.6	0.72	0.10	**< 0.001**
Drinking (%)	9.9^{a} ± 2.1	4.9^{ab} ± 1.2	3.6^{b} ± 0.9	5.0^{ab} ± 1.1	0.47	**< 0.05**	**< 0.05**
Resting (%)	39.1 ± 4.7	38.6 ± 4.3	32.6 ± 3.3	44.1 ± 5.0	0.14	0.81	0.14
Stretching (%)	0.4 ± 0.4	0.2 ± 0.2	0.4 ± 0.4	0.2 ± 0.2	0.59	0.92	0.94
Yawning (%)	0.2 ± 0.4	0.1 ± 0.1	0.3 ± 0.4	0.2 ± 0.3	0.80	0.47	0.88
Grooming (%)	14.0^{a} ± 2.2	6.8^{b} ± 1.2	16.5^{a} ± 2.1	12.5^{a} ± 1.8	**< 0.01**	**< 0.05**	0.14
Rearing (%)	1.6^{a} ± 0.3	3.7^{b} ± 0.4	1.5^{a} ± 0.3	1.9^{a} ± 0.4	**< 0.01**	**< 0.05**	0.09
Sniffing (%)	2.0^{a} ± 0.3	2.8^{ab} ± 0.3	3.7^{b} ± 0.4	3.9^{b} ± 0.5	0.19	**< 0.001**	0.25
Chinning (%)	1.9^{a} ± 1.1	0.1^{b} ± 0.1	0.5^{ab} ± 0.2	0.4^{ab} ± 0.3	0.07	0.78	**< 0.01**
Watching (%)	7.6 ± 1.2	6.7 ± 1.0	9.3 ± 1.3	8.8 ± 1.4	0.92	0.75	0.64
Allogrooming (%)	2.8^{a} ± 0.6	0.6^{b} ± 0.2	0.8^{b} ± 0.2	1.1^{ab} ± 0.4	**< 0.05**	**< 0.05**	**< 0.01**
Side-to-side (%)	33.7 ± 2.8	32.8 ± 2.6	32.7 ± 2.5	33.4 ± 2.8	0.98	0.93	0.75
Nose-to-nose (%)	0.5 ± 0.3	0.4 ± 0.3	0.2 ± 0.2	0.4 ± 0.2	0.94	0.53	0.56

$^{a-c}$ Means with different letters (a,b,c) in the same row differ significantly at an alpha value of 0.05

distinction, it would have been useful to differentiate between the rearing position linked to vigilance and the rearing position linked to curiosity, as rabbits were often observed to rear up towards an element of the environment, such as the fence for example. However, the observed difference in the expression of rearing (2,3% *vs* 1,1% of the observed time for PS119 *vs* 1001), even though significant, was small between both genotypes and any interpretation in this regard must be taken cautiously. The 1001 rabbits spent more time in the pens than the PS119 rabbits. Fetiveau et al. (2023) showed that PS119 rabbits more frequently expressed resting outside than 1001 rabbits, whereas 1001 rabbits more frequently expressed resting inside the huts. The 1001 rabbits may therefore have a less relaxed behavioural phenotype than PS119 rabbits when outside, and may be more frightened by external stimuli, as also suggested by their higher hair corticosterone level (Fetiveau et al., 2023). Another possible explanation is that 1001 rabbits, which are albino, might have a higher skin and eye sensitivity to UV rays (Fertl and Rosel, 2009; Stephenson et al., 2022) that would make them less well adapted to living outside if not provided with shelters than the coloured PS119 rabbits.

These results confirmed the importance of offering outdoor access to rabbits as it allows them to express a larger variety of specific behaviours; grazing being the predominant behaviour. Moreover, the dominance of grazing behaviour suggests it reflects a behavioural need in rabbit and restriction may impair their welfare as shown by Hugues et al. (1989). A challenge lies in choosing an optimal grass surface for animals given constraints faced by the farmer (land availability, number of animals, meadow's composition…). In our case, in the season studied, a 60-m^2 pasture area with 24 young rabbits seemed sufficient to allow them to graze continuously over the entire growing period. It is important to note, however, that while this area is sufficient to satisfy the need for grazing, it does not meet the nutritional needs of the animals. Additional supplementation with a complete feed is necessary.

5. Conclusion

This study provides new knowledge on the behavioural time budget of rabbits in a pen system with outdoor access and new non-invasive highly-visible marking method to study rabbit behaviour. With the help of this method, we documented a crepuscular behaviour of domesticated rabbits, which is similar to what has been observed in wild rabbits. Grazing was the predominant behaviour outside on the pasture, whereas resting was largely the predominant behaviour inside in the pens. A 60 m^2 pasture area enabled the rabbits to spend more time grazing than a 30 m^2 pasture area. Times spent on behaviours differed between genotypes, suggesting differences in the rabbits' perception of their environment. The results suggest selection programs (or cross-breeding schemes) could be used to produce a phenotype that is better adapted to the outdoor environment. Moreover, the results highlight the importance of offering rabbits as much outdoor grassy space as possible to allow them to express behaviours such as grazing for the duration of the rearing period.

Ethics approval

The 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 n° 115 of the Ministry of National Education, Higher Education and Research (approval number 16330–2018072716211212).

CRediT authorship contribution statement

Manon Fetiveau: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Visualization, Project administration. **Davi Savietto**: Conceptualization, Methodology, Validation, Investigation, Writing – review & editing, Visualization. **Andrew M. Janczak**: Validation, Writing – review & editing, Visualization. **Carole Bannelier**: Investigation. **Anne-Sophie Plagnet**: Investigation. **Mathilde Tauveron**: Investigation, Formal analysis, **Laurence Fortun-Lamothe**: Conceptualization, Validation, Writing – review & editing, Visualization, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2023.105872.

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