Novel phenotypes of feeding and social behaviour and their relationship with individual rabbit growth and feed efficiency

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A R T I C L E   I N F O

A B S T R A C T

Due to the lack of a recording system for individual consumption of group-housed rabbits, published studies about feeding behaviour are based on information recorded at the group- and not at the individual level and periods covering only a few days or, in some cases, only part of a day. Such information could be used to inform rabbit management systems but cannot be used for genetic selection. We aimed to generate and use information from a novel automated feeder for group-housed rabbits to identify new phenotypes for individual animals that could be incorporated into breeding programs to improve feed efficiency and social behaviour under different feeding regimens. At 39 d of age, rabbits from 15 batches were placed in cages and fed *ad libitum* to become used to the electronic feeder. From 42 to 58–59 d, one group of 1 086 rabbits was fed *ad libitum* (**AL**), while another group of 1 134 rabbits was fed on a restricted feeding schedule (**R**) by limiting the feeding time to the period between 1800 and 0600 h of the following day. We implemented a reliable multivariate method to remove anomalous feeding behaviour records. We then defined novel traits for feeding behaviour that apply to both types of feeding regimes, and for social behaviour that indicates an animal's rank within the cage hierarchy. We based these traits on feeder records and a biologically sound definition of a meal. Finally, we estimated the phenotypic correlations of those traits with growth and feed efficiency traits. Our findings demonstrate that variables about resource distribution among cage mates and an animal's priority for feed access were found to be good indicators of an animal's dominant or subordinate status within the cage. Based on results obtained in R animals (results were similar in AL animals), the most efficient animals were those that ate less frequently (phenotypic correlation with feed conversion ratio, rho = 0.6), and consumed smaller amounts per meal (rho = 0.7), spent less time at the feeder (rho = 0.4), and appeared to be subordinate, as they did not have priority access to the feeder (rho = −0.3), and had the smallest share of resources (range of rho = 0.2–0.6). We conclude that quantifying feeding and social behaviour traits can enhance the understanding of the mechanisms through which individuals exert their effects on the performance of their cage mates.

Implications

By using data from a novel automated feeder in two groups of rabbits, with and without feed restriction, we defined new feeding behaviour traits, some of them indicative of an animal's hierarchy within the cage. Variables related to resource distribution and an animal's priority for feed access reflected its dominant or subordinate status within a cage. The most efficient animals ate less often, consumed smaller meals, spent less time eating, and appeared to be subordinate, lacking priority access and having the smallest resource share. Information on these traits could be used to improve feed efficiency and/or social behaviour by breeding.

Introduction

Feeding behaviour (**FB**) could be defined as the pattern of feed consumption of an animal over a period. It is described by several variables that result from the information of records on the amount of feed consumed and the time when it occurs (Tolkamp et al., 2011). Measuring and characterising the FB of individuals or of a given population is important for fields such as animal health and welfare, nutrition, management and genetics. For

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example, knowledge of the consumption pattern of individuals within a population is necessary for the proper implementation of automatic feeding systems, regardless of whether rationing or *ad libitum* feeding is practised. On the other hand, individual and group information from FB allows for early detection of technical and environmental problems (drinking trough failures, inadequate temperatures, etc.) or subclinical diseases (Madsen and Kristensen, 2005). Genetic selection for improving disease resilience or resistance could also be done by selecting animals whose FB is less affected in the presence of disease/health challenges, as has recently been proposed for the drinking behaviour in pigs (Cheng et al., 2021). In addition, FB traits could be included in a selection index for improving feed efficiency in a breeding program, which is one of the main goals of livestock production systems (Dube et al., 2014). This strategy has been recently evaluated using a limited number of FB variables by Núñez et al. (2023) who found a slight improvement in the expected genetic response and the accuracy of the estimated breeding values in growing pigs.

Limiting the amount of feed given to animals during fattening is a common practice in rabbit production farms. This is done to minimize mortality rates linked to digestive disorders brought about by diseases like epizootic rabbit enteropathy (Gidenne et al., 2009). However, this practice may lead to other issues. In a study by Dalmau et al. (2015), the provision of feed at 75% of the *ad libitum* intake once a day led to the manifestation of agonistic behaviours such as biting, displacement, and animals jumping on top of each other during the entire fattening period. In addition, FB, feed efficiency and nutrient digestibility are affected by feed restriction as has been reported in several studies (Birolo et al., 2021; Martignon et al., 2021).

Previous studies have shown that during fattening, rabbits have a lower feed intake during daylight hours and that the rate of feed intake increases when they are subjected to hourly feed restriction (Tudela and Lebas, 2006; Martignon et al., 2021). Such information could be used to inform rabbit management systems, but these studies have several limitations such as feed consumption being measured at the group- and not at the individual level and for periods covering only a few days or, in some cases, only part of a day. This is due to the lack of a recording system for individual consumption of group-housed rabbits, as has been the case for several decades for other species. Recently, our group at the Animal Breeding and Genetics department at Institute of Agrifood Research and Technology (**IRTA**) (Caldes de Montbui, Barcelona, Spain) has designed and produced an automatic recording system for individual consumption of group-housed rabbits. The device not only records the timing and amount of feed consumption but also enables restricting the feed supply for specific periods as desired.

Using the information provided by IRTA's automated feeder, the main aim of this work was to study the relationship between growth and feed efficiency with classic and novel FB traits on the one hand, and with several indicators of the social position of the animal within the hierarchy of the group on the other. The overarching goal was to identify phenotypes, potentially novel ones, that could be incorporated into breeding programs, thereby enhancing the feed efficiency and social behaviour of group-housed animals. Additionally, this endeavour aimed to characterise the feeding behaviour of both efficient or inefficient, and dominant or submissive individuals, while exploring the connection between efficiency and social status.

The study was carried out in two rabbit populations of the same genetic origin, both selected for improved feed efficiency during the growing period, but following different strategies that involved the implementation of two different feeding regimens: *ad libitum* and time-based feed restriction. The objective was not to compare the outcomes between the populations and/or feeding regimens but to quantify the relationships between traits under feeding conditions that involve a different degree of competition among cage mates.

To achieve the above overarching aim, the following specific objectives were addressed: (i) to characterize the FB of the two rabbit populations subjected to different feeding regimes; (ii) to identify the FB parameters/traits that may be good indicators of the ranking of an individual within the social hierarchy, or its level of dominance among cage mates; (iii) to assess the relationship between growth and feed efficiency with the former traits as well as those that describe the individual feed consumption pattern. It was anticipated that the reported information would contribute to the development of management and breeding strategies for farm rabbits, as one would be able to easily and automatically measure traits that can be used to identify the most efficient or dominant animals without the need to visually monitor the animals or measure feed intake.

Material and methods

Animals and housing

The data correspond to animals from two selection lines, Average daily growth under feed restriction (**ADGR**) and residual feed intake (**RFI**), both selected to improve feed efficiency during fattening since June 2018 (6 generations) by different selection criteria: Average daily growth under feed restriction conditions (ADGR line) and residual feed intake (RFI line). The two lines originated at the same time (January 2017) from animals of the Caldes line founded in 1982 and selected for growth rate at fattening under *ad libitum* feeding in group-housed conditions (Piles et al., 2004).

The experiment was carried out at IRTA's nucleus farm at Caldes de Montbui, Spain. In this closed farm, the photoperiod was set to 16 light h/d (from 0700 to 2300 h) and the environmental temperature was kept at 20 ± 2 °C.

The study considered a total of 2 220 animals (1 086 and, 1 134 for ADGR and RFI lines, respectively) belonging to 15 batches born between March 2020 and May 2022.

At 39 days of age, the animals were placed in group housing cages, each accommodating 6 animals (370 cages: 181 ADGR and 189 RFI), measuring 76 cm width × 100 cm length × 32 cm height, and containing an electronic feeder. They previously occupied this cage with their dam, but in the absence of the electronic feeder. The electronic device was developed within the framework of the "Feed a Gene" European project (grant agreement no. 633531) and two nationally funded projects ("Genef" RTA2014-00015-C02 and "Genef2" RTI2018-097610-R-I00). It only allows one rabbit to eat at a time, due to the size of the front window through which the feed is accessed, in order to guarantee a proper identification of the eating animal. The feed supply device (Fig. 1) consists of a stainless-steel hopper that can hold up to 3.5 kg of feed, which is placed on top of a stainless-steel platform, under which the scale is located. At the base of the hopper and at a 45 ° angle, there is a plastic screw, which is rotated by a 12 V motor (14 rpm) to provide feed to the pan placed on the scale. This is done automatically once the weight of the feed pan is below a certain threshold. At the top end of the screw, a vertical tube directs the feed to the pan placed on the scale. The feeder does not have any structure to protect the rabbit from being pushed by others whilst eating. More details about the characteristics of the feeder can be found in the supplementary document https://www.feed-a-gene.eu/sites/default/files/documents/Feed-a-Gene_D2.2_rabbit_feeding_device.pdf.

At the onset of the fattening period (i.e., at 39 days of age), all animals were fed *ad libitum* to familiarise them with the feeder. The observation period was from 42 to 58–59 days of age (i.e.,

Fig. 1. Electronic feeder for rabbits.

16.6 days). During this period, RFI animals were fed *ad libitum* (**AL**) while ADGR animals were fed on a restricted feeding schedule (**R**) by limiting the feeding time to the period between 1800 and 0600 h the following day, including the night period when the rabbits are most active (Gidenne et al., 2010). Animals were fed a commercial pelleted diet (Piensos PICART; 15.5% CP, 2.3% fat, 17.2% crude fibre), and water was always available.

Each rabbit wore an ear transponder bearing a unique identification code (animal ID) that was recorded every time the animal entered and left the feed station using a radio frequency antenna system (125 kHz). In front of the feeder, there was a sensor activated when an animal was present. A visit to the feeder started when the sensor was activated and the antenna detected and read the animal transponder and ended when the animal left the feeder, the moment when the sensor was deactivated, and the transponder was no longer within the range of the antenna. The feeding device worked like a scanner, transmitting every second to a server the status of various sensors such as the scale and the radio frequency identification reader. The weight of the feed pan (recorded to the nearest 0.1 g), the transponder number of the rabbit, the time (recorded to the nearest second) and the feeder number were documented when a rabbit entered or left the feeder.

Growth and feed efficiency traits

The age of the animal (d) and its weight (g) were recorded at the beginning and the end of the follow-up period. From this information, the individual BW gain (**BWG**, in g) and experimental duration (**ND**, in d) were calculated as the difference in BW and age of the animal, respectively, at the end and the beginning of the follow-up period; average daily gain (**ADG**, in g/d) was calculated as ADG = BWG / ND. The feed conversion ratio (**FCR**, in parts of the unit) was calculated as the ratio between the average daily FI of

the animal in the follow-up period and its ADG. Finally, residual feed intake (RFI, g) was computed as the residual for each animal of the regression model of average daily FI on ADG and metabolic weight (**MW**) (i.e., $MW = \left(\frac{BWs + BWe}{2}\right)^{0.75}$) fitted within a batch. Terms BWs and BWe stand for body weight at the beginning of the follow-up period (42 d) and BW at the end of the follow-up period (58–59 d), respectively.

Data screening and aggregation of feeding events into meals

Records of cages with dead or culled animals, as well as records from the first and last day of the observation period that were incomplete, were excluded from the analysis. Data cleaning consisted of the elimination of records with missing values or wrong animal identifications, which represented less than 10% of the records. The lengths of the intervals between successive visits of the same animal (**IBV**; time elapsed in seconds between leaving the trough on one visit and entering the trough on the next visit) were then calculated from the retained records. To group data from visits to a feeder into feeding events (**FE**), a meal criterion was estimated (Howie et al., 2009). Thus, two consecutive visits with an interval between them shorter than this between-meal interval were considered to occur within the same FDE. The methodology proposed by Howie et al. (2009) was implemented for estimating the meal criterion for each animal. It is based on the analysis of changes in the *P* of animals starting to feed (**Pstart**) with the time since the last FE. For each animal and time t, the observed Pstart within the next minute is calculated as the number of intervals larger than t min and smaller or equal to t + 1 min divided by the number of intervals larger than t min. The meal criterion was estimated at the minimum point when Pstart is plotted against interval length. This value is estimated as the point at which the difference in Pstart changes from negative to positive values, using a rolling average over 5-min intervals to reduce the effect of random variation in values. The meal criterion was estimated for animals on R-fed and AL-fed separately. Because feed was not provided during part of the day in R-fed, only records corresponding to the feeding period (i.e., 1800–0600 h) were used to estimate the meal criterion for this group of animals.

Feeding behaviour traits

A brief description of all analysed traits is presented in Table 1. For each animal, records corresponding to different visits to the feeder within a FE were aggregated. Note that a FE may have resulted from grouping visits to the feeder where there had been no feed consumption. They will be referred to as "**empty meals**" hereafter and may relate to investigative behaviour. On the other hand, FE where there has been consumption will be referred to as "**meals**". The total number of FE (**NFE**) resulted from the addition of the number of meals (**NM**) and the number of empty meals. The rate of effective FE (**REFE**) was defined as the ratio between the NM and the NFE. The number of visits to complete a FE and a meal were defined as **NVFE** and **NVM**, respectively.

The time elapsed (seconds) between the start of the first and the end of the last visit in a FE or a meal were referred to as **TFE** and **TM**, respectively, while the time when the rabbit was effectively into the feeder was referred to as occupation time in a FE (**OTFE**, in s) or time eating (**TE**, in s) when it corresponded to a meal. The feeding rate (**FR**, in g/s) was computed as the ratio between the feed intake (i.e., the addition of the amount of feed consumed in each visit within a meal; **FI**, in g) and time eating (FR = FI / TE), while the feeding rate to complete a meal (**FRmeal**, in g/s) was defined for each meal as the ratio between the FI and TM. Finally,

Table 1

Abbreviations and descriptions of feeding behaviour, social behaviour and performance traits used or calculated for rabbits. When a trait was calculated, its calculation formula is given.

Type	Abbreviation	Definition	Formula	Units
Feeding behaviour				
	Empty meal	Feeding event with no feed consumption		
	Meal	Feeding event with feed consumption		
	NM	Number of meals		units
	NFE	Number of feeding events	$NFE = NM + \#\text{empty meals}$	units
	REFE	Rate of effective feeding events; the ratio between the number of meals and the number of feeding events	$REFE = \frac{NM}{NFE}$	units
	NVFE	Number of visits to the feeder to complete a feeding event		units
	NVM	Number of visits to the feeder to complete a meal		units
	TFE	Time elapsed between the start of the first and the end of the last visit within a feeding event		s
	TM	Time elapsed between the start of the first and the end of the last visit within a meal		s
	OTFE	Occupation time in a feeding event		s
	TE	Occupation time in a meal		s
	FI	Feed intake within a meal		g
	FR	Feeding rate	$FR = \frac{FI}{TE}$	g/s
	FRmeal	Feeding rate to complete a meal	$FRmeal = \frac{FI}{TM}$	g/s
	IBM	The interval between meals; the difference between the start time of two consecutive meals.		s
Social ranking				
	Position	The mean for all feeding events of the averages of the position in which each animal enters the feeder in each visit within a feeding event		units
	rateEM	The number of times an animal occupies the feeder without eating relative to the total number of feeding events in the cage	$rateEM = \frac{\sum_i^{ND} \frac{\# \text{ empty meals individual}}{NFE \text{ cage}}}{ND}$	Parts per unit
	rateFE	The average of the ratio of the number of feeding events of the animal relative to the total number of feeding events in the cage computed on a daily basis	$rateFE = \frac{\sum_i^{ND} \frac{NFE \text{ individual}}{NFE \text{ cage}}}{ND}$	Parts per unit
	rateFI	The average of the ratio of the feed intake of the animal relative to the total feed intake in the cage computed on a daily basis	$rateFI = \frac{\sum_i^{ND} \frac{FI \text{ individual}}{FI \text{ cage}}}{ND}$	Parts per unit
	rateT	The average of the ratio of the time spent in the feeder by an animal relative to the total time spent in the feeder by all cage mates computed on a daily basis	$rateT = \frac{\sum_i^{ND} \frac{OTFE \text{ individual}}{OTFE \text{ cage}}}{ND}$	Parts per unit
Growth and feed efficiency				
	ND	Number of days in observation		d
	TFI	Total feed intake in the monitoring period		g
	BWs	BW at the beginning of the follow-up period (42 d)		g
	BWe	BW at the end of the follow-up period (60 d)		g
	BWG	BW gain in the monitoring period	$BWG = BWe - BWs$	g
	ADG	Average daily gain	$ADG = \frac{BWG}{ND}$	g/d
	MW	Metabolic weight	$MW = \left(\frac{BWs + BWs}{2}\right)^{0.75}$	g
	FCR	Feed conversion ratio	$FCR = \frac{TFI}{BWG}$	units
	RFI	Residual feed intake		g

the length of the interval between meals (**IBM**, in s) was computed as the difference between the start time of two consecutive meals.

Outlier detection and removal

To remove anomalous records, data were processed separately for each genetic line. In the case of empty meals, occupation times with a value greater or smaller than 2 times the interquartile range above or below the 75th and 25th percentiles of the data, respectively, were eliminated. In the case of meals, outliers were removed according to the robust Mahalanobis distance criterion obtained for the variables TE, FI, and IBM. Thus, we first computed the robust distance of each observation ($x_i, i = 1 \cdots n, x_i \in R^p$ where n and p are the number of data and variables (i.e., 3), respectively) to the mean of the multivariate Gaussian distribution of the data as:

$$rd(\mathbf{x}_i) = \sqrt{(x_i - \mu_{mcd})' S_{mcd}^{-1} (x_i - \mu_{mcd})}$$

In the above equation, μ_{mcd} and S_{mcd} are the robust Minimum Covariance Determinant estimates of the mean vector and covariance matrix, respectively, of the multivariate Gaussian Distribution of the data. Those parameters were obtained from the data as the mean and the covariance of the 75% subset of data whose covariance matrix has the smallest determinant (i.e., the subset of the data that is most tightly distributed) using the function cov.mcd

of the MASS Package of R (Team, 2020). Then, x_i was declared to be an outlier if $rd(x_i) > 5 \times \sqrt{\chi^2_{p,0.999}}$ in which $\chi^2_{p,0.999}$ is the χ^2 critical value that corresponds to a 0.001 significance level and 3 df.

Once outliers were removed, for each FB trait, daily values were obtained by summing the values corresponding to each day and animal while hourly values were obtained by summing the values corresponding to each hour and animal and dividing by the number of days (i.e., 14 d, from day 2 to day 15).

Social ranking traits for an animal within the cage group

For all visits of the cage mates having the same number of FE (see an example in Fig. 2), the order/position in which each animal accessed the feeder was recorded and standardized by subtracting the minimum value (i.e., 1) and dividing by the range (i.e., total number of cage mate visits corresponding to a specific number of FE − 1). The standardization was needed because the total number of visits corresponding to different FE in a cage differed (for instance, accessing the feeder in the order 4 out of 5 visits, as opposed to 4 out of 25 visits cannot be considered similar). From this information, the mean of the standardized order corresponding to the successive visits to complete every FE was calculated for each animal. This variable was then averaged for all FE carried out by each animal throughout the follow-up period. We refer to this trait of the animal as **Position**.
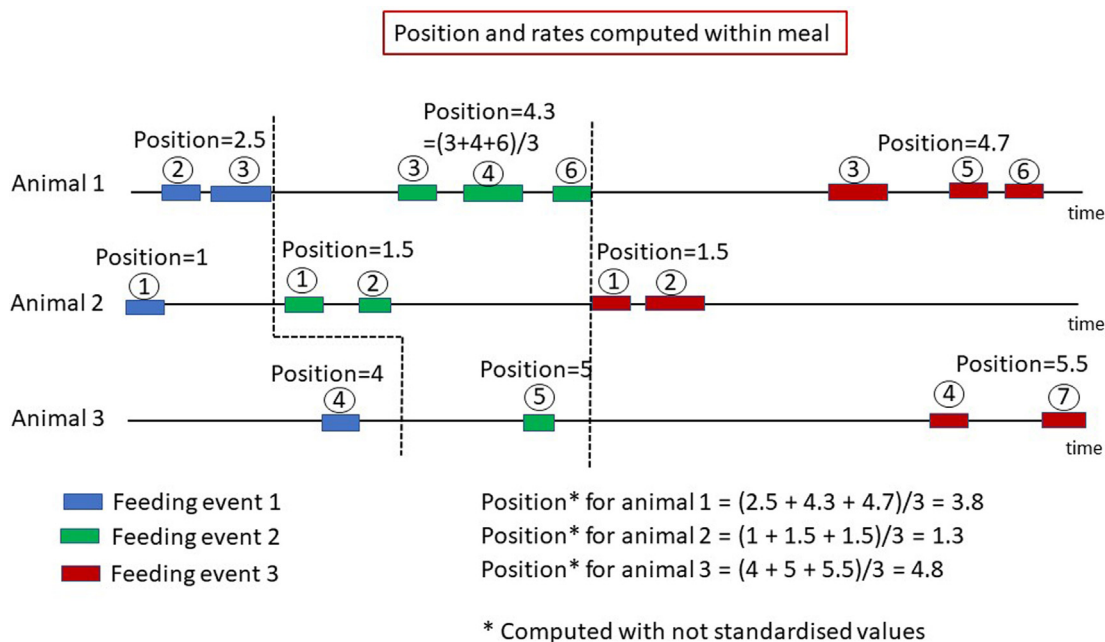
Fig. 2. Graphic representation of visits (rectangles) and feeding events (same colour visits) and computation of the position variable with no standardization of visit records (number in a circle), for the sake of simplicity, for a hypothetical cage with 3 rabbits.

On the other hand, also for each feeder and day of the observation period, the distribution among the cage mates of the total number of FE (**rateFE**), the total amount of time spent in the feeder (**rateT**) and the total feed intake (**rateFI**) were calculated as the ratios between the total values corresponding to each animal in the cage relative to the total values corresponding to all cage mates in each specific day. This unit of time (i.e., day) was used considering that it represents a complete circadian cycle (Szendrő et al., 2016) and that animals could eat at different times during the day trying to accommodate the preferences of dominant cage mates. The number of times an animal occupied the feeder without eating (empty meals) relative to the total NFE in the cage (**rateEM**) was also calculated. All of the above traits were assumed a priori to be related to the degree of dominance of the animal over its cage mates given that, at this stage of their life, young rabbits mainly compete for the use of (scarce) resources (feed and time at the feeder). Finally, the within-cage CV of the previous daily ratios was calculated for each cage and day of the follow-up period. A higher CV would indicate greater differences between animals in the way resources are distributed.

Statistical analyses

For each genetic line, the separate Pearson correlations between the individual averages of social ranking traits as well as with individual averages of feeding behaviour, growth and feed efficiency traits were calculated using the function "cor()" of the library "DescTools" of R (Signorell, 2023).

Results

Growth and feed efficiency traits

Table 2 shows descriptive statistics of growth and feed efficiency traits in the two rabbit populations.

Ad libitum-feeding group
The BW of the AL-fed rabbits increased by 742.6 g during the follow-up period, which implies an increase of almost 1.6 times

the initial weight from 42 d (1 295 g) to 58–59 d (2 038 g) at a rate of 45 g/d. The mean (SD) of daily feed intake (**DFI**) and FCR were 120.6 g/d (36.8 g/d) and 2.8 (1.1), respectively.

Restricted-feeding group
The BW of R-fed rabbits increased by 641.9 g, entailing an increase of almost 1.5 times the initial weight (1 287 g) at a rate of 39 g/d. The mean (SD) of DFI and FCR were 86.2 g/d (33.0 g/d) and 2.3 (0.9), respectively (Table 2).

Interval lengths between visits and meal criterion definition

Ad libitum-feeding group
Fig. 3A shows histograms of the interval length between visits in natural logarithmic scale [i.e., ln(IBV)] for AL animals. These histograms were obtained for intervals corresponding to every week of the experimental period. The frequency decreased rapidly with increasing interval length to reach a minimum of 12.1s. After this point, there were two peaks around 42.5s and 20.2 min, respectively.

Fig. 3 panel C shows the median of Pstart calculated for intervals between visits up to 60 min. Pstart decreased rapidly at short intervals and then increased from approximately 9-minute interval length corresponding to the median of the meal criterion. For animals on AL, Pstart remained relatively constant from this point onwards.

Restricted-feeding group
Fig. 3B shows histograms of the interval length between visits in natural logarithmic scale obtained for intervals corresponding to every week of the follow-up period for R animals. The frequency decreased rapidly with increasing interval length to reach a minimum of 11.5 s. After this point, there were two peaks around 40.5 s and 19.8 min, respectively.

Pstart (Fig. 3 panel C) decreased rapidly at short intervals and then increased from approximately 9-minute interval length corresponding to the median of the meal criterion. Then, it increased with the duration of the interval until it reached a maximum of 25 min and then decreased again.

Table 2

Descriptive statistics of growth and feed efficiency traits in *ad libitum* (AL-fed) and restricted fed (R-fed) rabbit populations.

Trait[1] (units)	R-fed		AL-fed	
	Mean	SD	Mean	SD
ADFI (g/d)[2]	86.2	33.0	120.6	36.8
FCR (parts per unit)	2.27	0.92	2.75	1.09
ADG (g/d)	38.8	7.3	44.9	7.5
BWs (g)	1 286.7	206.7	1 295.4	204.2
BWe (g)	1 928.6	241.4	2 038.1	228.4

[1] ADFI: Average daily feed intake; FCR: feed conversion ratio FCR = ADFI/ADG; ADG: average daily gain; BWs: BW at the start of the fattening period; BWe: BW at the end of the fattening period.

[2] Expressed as fed basis.
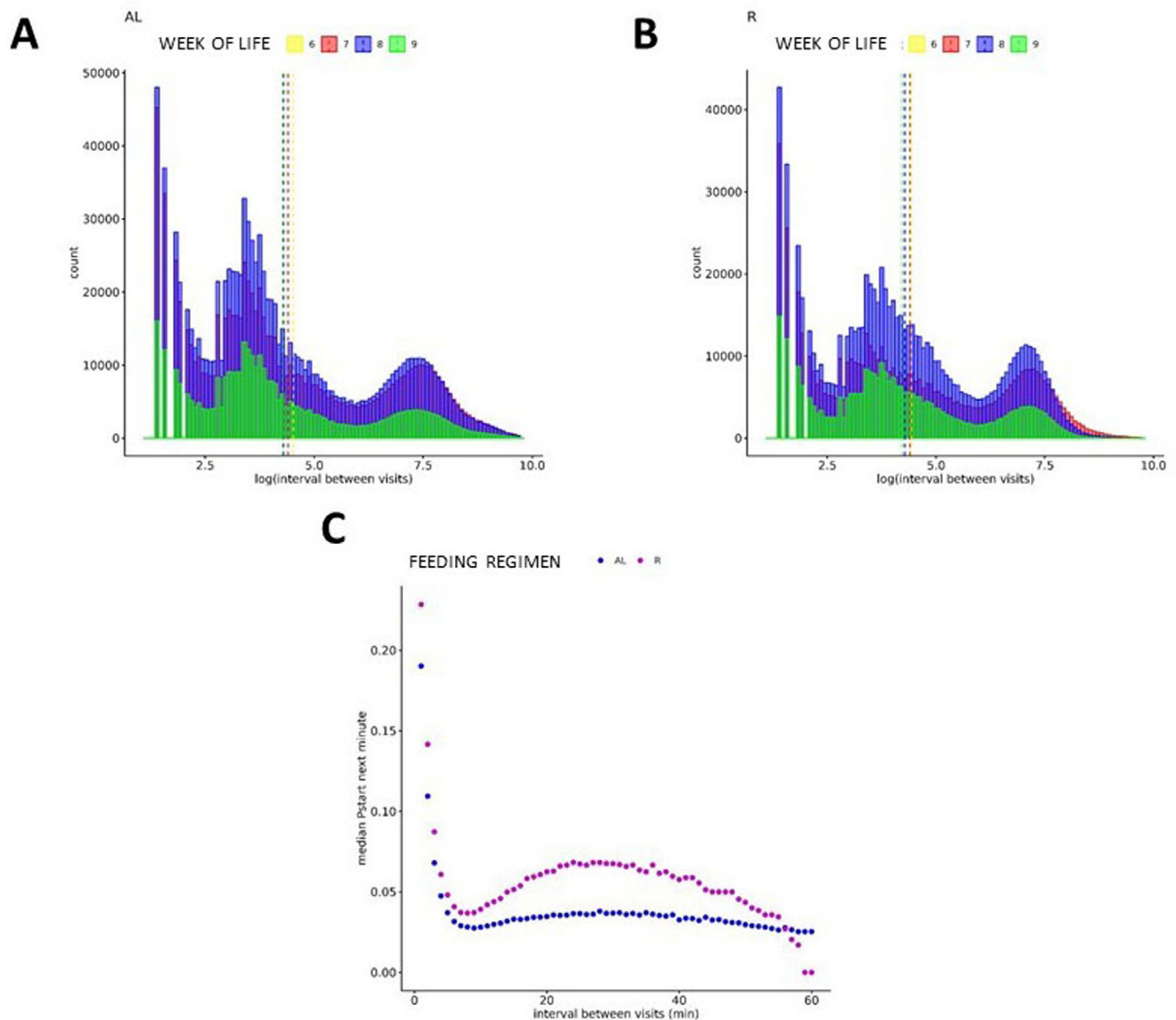
Fig. 3. Histograms of the interval length between visits, as log(IBV) for rabbits fed *ad libitum* (AL, panel A) or restrictedly (R, panel B) and *P* of animals starting a visit depending on the interval between visits (panel C).

Feeding behaviour

Ad libitum-feeding group

The evolution of feeding behaviour traits over the fattening period is shown in Fig. 4. The NFE (panel A) was 25 at the beginning of the observation period increasing with time until it reached a maximum of 28 FE on day 11, and then remained constant. The NVFE also increased with time (Fig. 4 panel C) reaching a maximum on day 14. The daily pattern of NFE is shown in Fig. 4, panel B. On average, AL animals had 1.3 FE per hour from 0000 to 0600 h, which gradually reduced to reach a minimum of 0.7 FE per hour at 15 h. From this moment onwards, they gradually increased the number of FE until they reached a value of 1.3 by 24 h. The NVFE averaged 4.2 per hour and was similar regardless of the time of the day (Fig. 4 panel D).

The NM, TM, and FI were 23 meals/d, 3 hours/d and 121.6 g/d on average, respectively (Fig. 5 panels A, B and C). The daily feeding rate, calculated as FI (in g) divided by time to complete a meal (TM, in s), reached its maximum at day 15 with a value of 0.021 g/s (Fig. 5 panel D).

Regarding the daily pattern, the maximum NM was around 1.2 from 0000 to 0600 h and from 2100 to 2400 h (Fig. 6 panel A). It decreased gradually from 0600 h to reach a minimum of 0.6 meals at 1500 h and then increased until 2300 h. The hourly TM averaged 8.3 min with a minimum of 5.8 min at 1500 h. The pattern was the same for hourly FI (Fig. 6 panel C) as for hourly NM (Fig. 7 panel A). The maximum was around 5.6 g/h in the first 6 h of the day, then decreased to 3.3 g/h at 1500 h, and finally increased to reach 5.8 g/h again at 2300 h. The hourly FRmeal was almost constant during the whole day being on average 0.018 g/s (Fig. 6 panel D).

Restricted-feeding group

During the fasting period, R animals went to the feeder a few times and spent very little time there (Fig. 7). The number of visits to the feeder during this period of the day is not comparable with the number of FE during the feeding period because different criteria were used to aggregate consecutive accesses to the feeder into visits or FE (10s and the meal criterion for fasting and feeding period, respectively). During the first days of the observation period, the R animals went to the feeder on average 21 times per day dur-
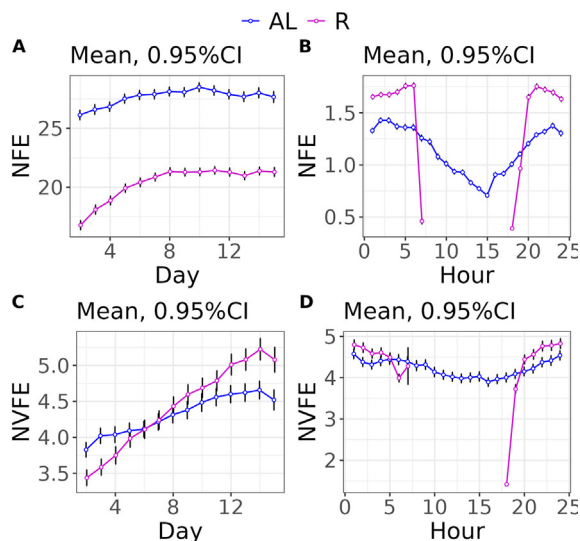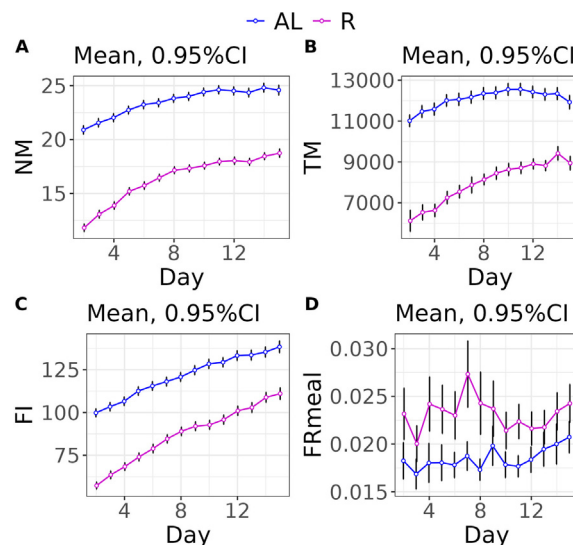

Fig. 5. Daily evolution of the number of meals during feeding time (NM, panel A), the time elapsed between the start of the first and the end of the last visit in a meal (TM, in s, panel B), feed consumed in a meal (FI, in g, panel C) and feeding rate to complete a meal (FRmeal, in g/s, panel D) throughout the fattening period, for rabbits fed *ad libitum* (AL) and restrictedly (R). CI: confidence interval.
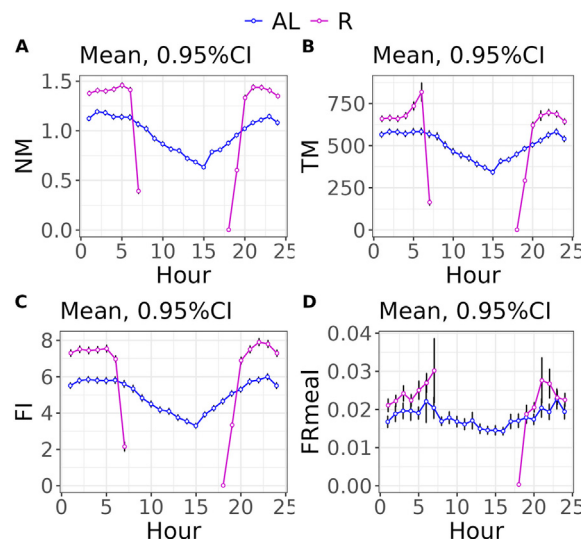

Fig. 6. Hourly evolution of the number of meals during feeding time (NM, panel A), the time elapsed between the start of the first and the end of the last visit in a meal (TM, in s, panel B), feed intake (FI, in g, panel C) and feeding rate to complete a meal (FRmeal, in g/s, panel D) throughout the fattening period, for rabbits fed *ad libitum* (AL) or restrictedly (R). CI: confidence interval.

ing the fasting period. This value decreased rapidly with time to reach a minimum of 11 times per day around day 8. The occupation time during the fasting period followed the same pattern as the number of visits to the feeder. On average, R animals spent very little time in the feeder during the fasting period (on average less than 5 min/d from day 8).

Regarding the evolution of feeding behaviour traits over the fattening period (Fig. 4), the NFE (panel A) at the beginning of the observation period was 15 in R rabbits. This figure increased with time until it reached a maximum of 21 FE on day 8 and then remained relatively constant. The NVFE also increased with time (Fig. 4 panel C) from 3.4 (day 2) to 5.4 (day 14). Regarding the daily pattern (Fig. 4 panel B), on average, R animals had 1.6 FE per hour throughout their whole feeding period (i.e., from 0000 to 0600 h
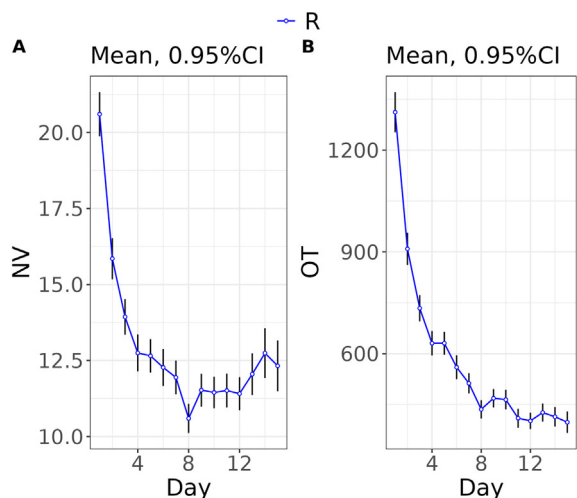

Fig. 4. Daily and hourly evolution of Number of feeding events (NFE panels A and B, respectively) and Number of visits to the feeder to complete a meal (NVFE panels C and D, respectively) throughout the fattening period, for rabbits fed *ad libitum* (AL) or restrictedly (R). CI: confidence interval.

Fig. 7. Evolution of the number of visits (NV, panel A) and occupation time (OTFE, in s, panel B) during the fasting time throughout the fattening period for restrictedly-fed (R) rabbits. CI: confidence interval.

and from 1800 to 2400 h). At the time when the feed supply was interrupted, the number of FE rapidly decreased, whereas it increased again rapidly when the feed supply was restored to reach again a value of 1.6 FE per hour on average. The NVFE (Fig. 4 panel D) was on average 4.7 per hour, except just at the time when the feed supply was restored after fasting when it reached very low values (1.5 per hour).

The NM, TM and FI in R rabbits were 16 meals/d, 2.2 h/d and 87 g/d on average, respectively (Fig. 5 panels A, B and C). The daily FRmeal reached its maximum at day 7 with a value of 0.027 g/s (Fig. 5 panel D).

Regarding the daily pattern, the NM in R rabbits was around 1.4 in one hour for the whole feeding period except when the feed supply was interrupted or restored (Fig. 6 panel A). The hourly TM averaged 9.3 min in R (Fig. 6 panel B), but it reached a maximum just before the feed supply was interrupted at 0600 h. The hourly FI (Fig. 6 panel C) was on average 7.25 g/h with a maximum of 7.9 g/h at 2200 h. The hourly FRmeal was on average 0.022 g/s (Fig. 6 panel D).

Markers of social ranking or dominance among cage mates

The within-cage CV of the daily NM, TM, FI and FRmeal is shown in Fig. 8. Similarly, Fig. 9 shows the within-cage CV of the daily rateFE, rateEM, rateT and rateFI.

Ad libitum-feeding group

The value for NM and TM was almost constant over the follow-up period (Fig. 8 panel A and B). However, the CV of FI (Fig. 8 panel C) and FRmeal (Fig. 8 panel D) were slightly higher after mixing animals from different litters at weaning and decreased gradually throughout fattening until days 8 and 10, respectively, when remained constant.

The within-cage CV of traits related to the distribution among cage mates of the number of FE, the OT and the FI (rateFE, rateT and rateFI, respectively) for each day throughout the follow-up period was also constant in AL rabbits (Fig. 9 panels A, C and D). However, rateEM followed an increasing pattern with values ranging from 0.5 to 0.68 on day 15 of the follow-up period (Fig. 9 panel C).
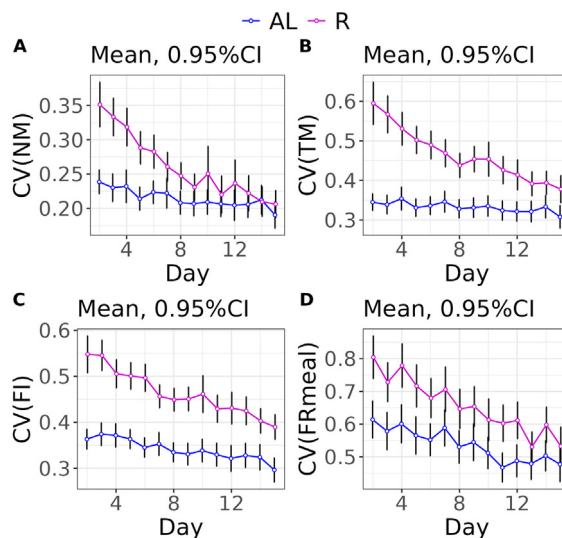
Fig. 8. Daily evolution of the CV for number of meals during feeding time (NM, panel A), time elapsed between the start of the first and the end of the last visit in a meal (TM, panel B), feed intake (FI, panel C) and feeding rate to complete a meal (FRmeal, panel D) throughout the fattening period, for rabbits fed *ad libitum* (AL) or restrictedly (R). CI: confidence interval.
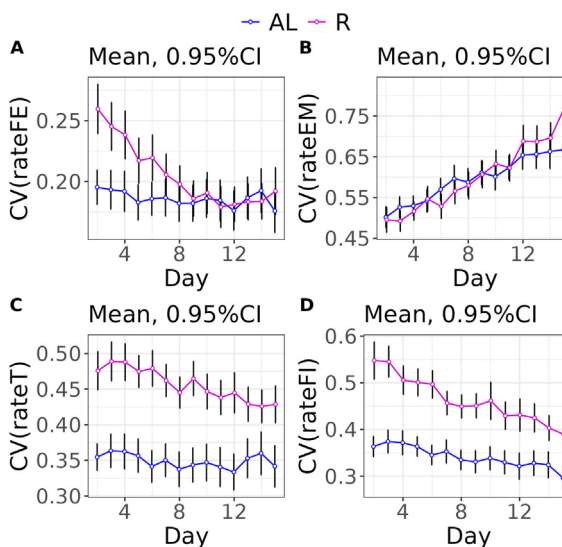
Fig. 9. Daily evolution of the variation coefficient for the average of the ratio of the number of feeding events of the animal relative to the total number of feeding events in the cage (rateFE, panel A), the number of times an animal occupies the feeder without eating relative to the total number of feeding events in the cage (rateEM, panel B), the average of the ratio of the time spent in the feeder by an animal relative to the total time spent in the feeder by all cage mates (rateT, panel C) and the average of the ratio of the feed intake of the animal relative to the total feed intake in the cage (rateFI, panel D) throughout the fattening period, for rabbits fed *ad libitum* (AL) or restrictedly (R). CI: confidence interval.

Restricted-feeding group

In R rabbits, the CV of the daily NM, TM, FI and FRmeal (Fig. 8) followed a decreasing pattern throughout the fattening period with numerically higher values than those described for AL rabbits. The highest values were found for the CV of FRmeal which reached a value of 0.8 at day 2 of the follow-up period (Fig. 8 panel D).

The values of the CV of rateEM increased with time from 0.49 on day 2 to 0.77 on day 15 (Fig. 9 panel B). This was the trait that showed the most variation in the two groups of animals. However, rateFE, rateT and rateFI showed a decreasing pattern from the beginning of the follow-up period (Fig. 9 panels A, C and D). Of

these 3 traits, rateFI and rateT showed greater variation than rateFE.

Phenotypic correlations between the three groups of traits

Phenotypic correlations in R rabbits are shown in Fig. 10 and are the only ones discussed. Results corresponding to AL animals can be found in the Supplementary File S1. The patterns of the correlations between the various traits were very similar for both groups of animals, although no comparisons were made.

Growth traits (i.e., weaning weight -, and ADG) were not correlated with either FB traits or markers of hierarchical position or dominance of cage mates. As expected, those traits were not correlated with RFI and were poorly correlated with FCR (maximum of −0.3).

The most phenotypic correlations among FB traits were globally low (0–0.5 in magnitude). However, these correlations were high between IBM with NM and NFE (−0.8) and NM and NFE (+0.9); moderate to high between FI and NVM (0.7) and between REFE and NM, NVM and IBM (0.6, 0.7 and −0.6, respectively). The values of these correlations are the expected values according to the trait definitions themselves.

The FI was the most correlated variable with FCR and RFI (0.7 and 0.8, respectively) with the most efficient animals eating the least. The FRmeal was slightly negatively correlated (−0.2) with NFE and with both FCR and RFI, with the most efficient animals eating at a faster rate. The occupation time within a FE (OTFE) was poorly correlated with RFI (0.1) and not correlated with FCR. However, REFE, FI, TM, IBM, NVM, NM and NFE were moderate to highly correlated with RFI and FCR. Thus, the most efficient rabbits were those that, on average, visited the feeder less frequently

to complete a meal, ate fewer meals, spent less time in the feeder and let more time pass between meals and had lower REFE.

Regarding markers of hierarchical position or dominance of cage mates, the correlations between all of them were very variable. The correlations between the markers of hierarchical position or dominance of cage mate varied substantially. They were very low between rateEM and rateFI and rateT (−0.2), low between rateEM and rateFE (0.4), moderate between rateFE and rateFI (0.6) and rateT (0.5), and high between rateFI and rateT (0.9). Thus, the animal that ate most of the feed consumed within a cage was the one that spent the most time at the feeder. On the other hand, the animal that went most frequently to the feeder was the one that had more empty meals than its cage mates. The position was negatively and moderately correlated with all the other markers (ranging from −0.4 to −0.6) except with rateEM (−0.1). Thus, an animal that ate first was an animal that, on average, occupied the feeding trough more times, spent more time in the feeder and ate a larger amount of the feed provided each day than its cage mates.

The correlation between the position and feed efficiency traits was −0.3 and −0.4 for FCR and RFI, respectively. Thus, the animals that ate first were less efficient in transforming feed into BW gain. The relationship between all the other markers of the dominance of cage mates and RFI and FCR was very similar. A more efficient animal went to the feeder less often, spent less time at the feeder and ate less of the feed consumed in a day than its cage mates.

The correlation between the social position and all the other markers of dominance with feeding behaviour traits was moderate to low, except between rateEM and REFE and between rateFI or rateT and FI, as expected according to the trait definitions themselves. Thus, the animals that ate first, ate more times and had less time elapsed between meals. On the other hand, on average, animals that ate more feed than their cage mates within a day were also those that visited the feeder more often to complete a meal, took more meals and waited less time between meals during the whole follow-up period compared to their cage mates.

Discussion

The main objective of this study was to establish the phenotypic relationship between feed efficiency and different behavioural variables that are easily obtained from the information recorded by the electronic feeders. The ultimate goal was to define phenotypes, possibly new ones that could be included in breeding programs to improve feed efficiency of animals housed in groups, but also to characterise the feeding behaviour of an efficient animal and a dominant/submissive animal, as well as to determine the relationship between efficiency and dominance. The objective was addressed in two lines of rabbits with a common genetic origin selected for feed efficiency following different strategies which involved different feeding regimens: *ad libitum* or time-based feed restriction. As a result of the 6-generation selection process, the genotypes of the animals were likely to differ slightly between lines. We aimed to understand the relationships between feeding behaviour, social position associated with feeding within the cage (hierarchy), and growth and feeding efficiency that may arise from each regimen/ line. No comparisons between the two lines were made due to the confounding between the feeding regimen and genotype.

Feed restriction is often applied on rabbit farms to prevent digestive disorders, thereby reducing mortality and morbidity, and improving the feed efficiency of growing rabbits (Gidenne et al., 2012; Birolo et al., 2020a,b, 2021). The feeding behaviour of rabbits has been studied very little and never using individual records of rabbits housed in groups. The few studies that exist only
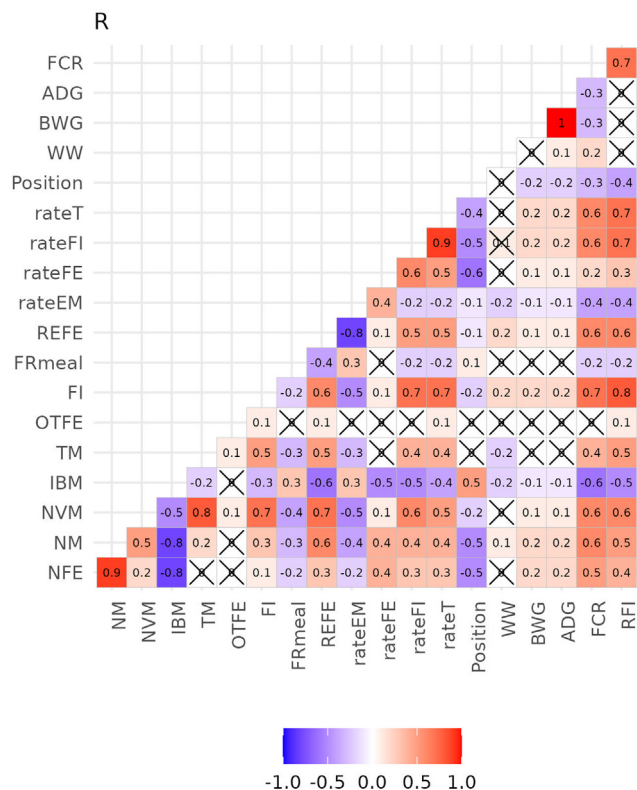
Fig. 10. Phenotypic correlations between performance, feeding and social behaviour traits in restricted fed (R) rabbits. WW: weaning weight (g). See Table 1 for other abbreviations.

evaluated a few variables such as the number of visits to the feeder, feed intake, time spent in the trough and feeding rate (Gidenne et al., 2010; Birolo et al., 2020b). This is despite the fact that feeding behaviour may relate to several of the productive traits and especially feed efficiency (Rauw et al., 2006). The reason for this is that no electronic feeders have been available for rabbit species to enable the capture of such traits, in the manner done for other species (e.g., pigs or cattle) for several decades now. Such a device has been recently developed and produced by our research group and used in the present study, which opens the possibility of studying feeding behaviour from individual records in group-housed rabbits under different feeding regimes.

The following novel methodological achievements were reached from the above aims:

1. New definitions of feeding behaviour traits were developed and obtained, once a definition of meal was established for each animal, following a methodology never previously implemented. For example, we defined the time an animal needs to complete a meal which is not equal to the sum of the trough occupancy time usually calculated, or the ratio of FE in which the animal actually eats, among other variables.
2. Also based on the definition of a meal, we calculated the average position in which each animal accessed the feeder at each meal, and the rate of feed and time spent at the feeder out of the daily total in the cage that corresponds to it. The former variables could be indicators of the degree of dominance/subservience of the animal with respect to its cage mates, as it can be considered that at the beginning of the growth stage, animals mainly compete for available scarce resources. This is different from the classical dominance traits referred to in the literature (Farabollini, 1987), associated with competition for other resources, such as mating. Such traits have never been described before and are shown here to be useful given their relationship with feed efficiency.
3. A novel method for the elimination of outlier values of feeding behaviours using robust multivariate methods was established. Past studies use arbitrary values or univariate methods. Univariate methods rely on assumptions of normality and can be sensitive to departures from this assumption, leading to inaccurate outlier detection. In addition, univariate methods can be heavily influenced by extreme values in a single variable, leading to unstable results. However, multivariate robust methods are designed to handle datasets that do not conform to strict assumptions of normality which are common in real-world data. Such methods consider the overall structure of the dataset, making them less susceptible to the impact of isolated extreme values and providing more robust estimates of central tendency and dispersion. By considering the relationships between variables, these methods can distinguish between genuine outliers and observations that may appear extreme in a univariate context but are within the expected range given the multivariate structure (Hawkins, 1980)

It is important to emphasize that all these methodological advances were made using individual information from rabbits whilst housed in groups, which is completely novel for this species. On the other hand, our results are not comparable to others where the feed intake in rabbits is also measured because of the different feeding regimens, age and breed of the animals, the definition of a meal, and especially the way in which data are recorded. Therefore, just as we avoided making comparisons between the selected genetic lines, we believe that comparisons with other papers are not valuable.

The analysis of feeding behaviour is probably not affected by the technique used to measure it (e.g., visual observations, jaw movements, or electronic feeders) if an appropriate definition of a meal is used as the basic unit of daily feed behaviour, instead of short FE or visits to the feeder (Tolkamp et al., 2000; Howie et al., 2009). This is because short-FE seems to be distributed randomly in time, whereas meals appear to be dictated by physiological principles, such as hunger and satiety (Tolkamp et al., 2011). The threshold used to group data from visits to a feeder into meals (named "meal criterion") has a huge impact on the parameters that define FB and, therefore, on the conclusions drawn for meal pattern analyses. The meal criterion represents the shortest interval between visits that can be considered to be between separate meals. Throughout different studies, this criterion has been estimated following different methodologies that have been discussed in detail by Tolkamp et al. (1998). Considering that satiety is high at the end of a meal, the P of an animal starting to eat immediately after finishing a meal is low and increases with the time elapsed since then. This pattern is not found when visits to the feeder are used as units of feeding behaviour (Howie et al., 2009).

Based on this idea, Howie et al. (2009) defined the meal criterion as the minimum point when the P of animals starting to feed since the last FE was plotted against interval length. This method was chosen in our study because it agrees with biological principles of short-term feed intake regulation and because it is not necessary to identify the functions that describe the distribution of within- and between-meal intervals. In addition, the method properly describes the frequency distributions of intervals between meals in several species (Tolkamp et al., 1998). It should be noted that the method was developed to apply to animals given *ad libitum* access to a feed. In this paper, we show that the method can, within limits, be applied to define the feeding behaviour of animals fed restrictedly. Previously, the method has been applied to analyse the feeding behaviour of cows given access to bulky feeds (Tolkamp et al., 2002). This is equivalent to feed restriction, as a bulky feed is expected to restrict the feed intake of animals, albeit voluntarily.

In our study, feed restriction was carried out by limiting the time of feed supply to 12 h, from 1800 to 0600 h of the following day, trying to adjust to the rabbit peak activity period, which occurs during the night (Gidenne et al., 2010). This assumption was confirmed by our records on AL-fed rabbits (Fig. 6 panel B) who reached a maximum of FE at 0200 h. and a minimum at 1500 h. The preference for certain times for feeding is the result of the effects of several physiological factors, such as metabolic processes and hormonal circadian rhythms (Strubbe and van Dijk, 2002), probably associated with the adaptive advantage that a preyed species has nocturnal activity in its natural environment. This could increase fights for feed among cage mates (Boumans et al., 2018), especially if feed is a limited resource. However, it should be noted that even when feed is freely available, as in the case of AL rabbits, it can still be considered a scarce resource, as animals may compete for access to the feeder and the dominant animals may actually obstruct access to it (Nielsen, 1999).

The meal criterion was estimated separately for each individual of each group of animals. Because feed was not provided during part of the day in R-fed animals, only records corresponding to the feeding period were used to estimate the meal criterion for this group of animals. The P of starting a visit (Pstart, Fig. 3 panel C) increased as the time from the previous visit increased for R-fed animals. This is to be expected by the principles of hunger and satiety. Interestingly, the same P did not increase as substantially for AL-fed animals (Fig. 3 panel C), making the definition of a meal for this animal less straightforward. Morgan et al. (2000) suggested that this can be an artefact of how feeding behaviour data are aggregated, and suggested that in the case of pigs, disaggregation of the data into day and night feed visits to the feeder resulted in meal criteria that were consistent with the concepts of hunger

and satiety. Such a 'disaggregation' was artificially imposed by the R feeding regime, and it is perhaps due to this that the feeding behaviour of these animals is consistent with these principles.

Rabbits under time-based feed restriction quickly adapted to the feeding period, only visiting the feeder a few times a day, after the 5th day, reaching a minimum of 11 visits around day 8, and staying very little time in there (around 5 minutes a day on average; Fig. 7) during the fasting period.

In addition to adapting to the feeding period, animals must adjust their feeding behaviour according to the social position they hold within the group, i.e., their level of dominance over cage mates (Nielsen, 1999). Thus, once such hierarchy is established, subordinate animals adapt their feeding behaviour according to the preferences of the dominant animals and eventually consume and spend time at the feeding trough at a different time of the day. Subordinate rabbits might have to wait until the dominant rabbit has finished eating before they can access the feed. Thus, at the start of the observation period, R-fed rabbits required fewer visits to finish a FE compared to AL-fed rabbits, but after 7 days, the situation reversed, with AL-fed rabbits requiring fewer visits to complete a meal than R-fed rabbits. This could be because, at this point, the R-fed cage mates have already established their hierarchical relationships and have learned what the daily feeding period is. In addition, they need to satisfy their increased nutrient requirements as a result of growth by visiting the feeder more often and staying at the feeder longer during the short period of the day when feed is available. The establishment of hierarchical relationships is reflected in the within-cage CV of the variables NM, TM, FI and FRmeal (Fig. 8), which are high 3 days after mixing the animals from different litters at weaning and decreased progressively throughout the follow-up period in R-fed rabbits. The pattern over the number of days of the within-cage CV of rateFE, rateT and rateFI (Fig. 9, panels A, C and D) also supports this idea. There is more variation in the distribution of time and feed at the beginning of the fattening period in R-fed rabbits which are subject to stronger competition for feed than one week later.

Our final objective was to assess the relationship between feeding and social behaviour traits, and between growth and feed efficiency with feeding behaviour traits. The correlation between the social position and the variables rateFE, rateFI and rateT in R rabbits were negative and moderate. Thus, the animals that have priority access to feed (i.e., lower position values) are those that eat most of the feed, occupy the trough most of the time and have most of the meals in a day. These behaviours can be considered typical of dominant growing rabbits, who will often assert their dominance over other rabbits by controlling resources like feed. In addition, those who had priority access to the feed were those that ate more times (higher NFE and NM), leaving shorter intervals between meals, and consumed more feed in each meal. Subordinate rabbits eat faster than dominant rabbits. The value of the correlations of the variables rateEM, REFE, rateFI, rateT and position with FRmeal, although low or very low, was statistically significant and point towards this.

The feeding behaviour of more efficient rabbits was characterized by a lower NFE, NM, REFE, NVM, FI and TM. On the other hand, animals that can be considered dominant (i.e., have a higher value of the variables rateEM, rateT, rateFI and rateFE and a lower value of the variable position) were the least efficient (i.e., have a higher RFI and FCR). This could correspond to a higher energy expenditure to maintain their dominant position or to the fact that the higher intake could be related to more fat deposition so there is a deterioration in FCR. In addition, considering that feed restriction seems to be associated with an improvement in feed efficiency (Foubert et al., 2007; Duperray and Guyonvarch, 2013; Knudsen et al., 2014; Gidenne et al., 2017; Birolo et al., 2021), dominant rabbits could be producing an effect on the feed efficiency of their cage mates by limiting the amount of feed they can eat.

Only Herrera-Cáceres et al. (2020) have explored the relationship between feed intake, occupation time and feeding rate in growing pigs fed *ad libitum*, with social interaction effects (i.e., the effect that an animal exerts over its cage/pen mates) on growth, feed efficiency and backfat thickness. However, as far as we know, no study to date has explored the usefulness of the information provided by electronic feeders to define variables that are potential markers of the level of dominance that an individual exerts over its cage or pen mates, in rabbits or indeed any other species. It is, therefore, necessary to know the mechanisms through which an animal exerts its effect on its cage mates because this could help to improve genetic selection processes to obtain animals that exert a positive or at least a non-negative effect on the group.

Conclusions

We used a novel automated feeder to quantify traits related to the feeding behaviour and social behaviour of rabbits and to develop hypotheses about the relationship of these traits with the outcomes of growth and feed efficiency. Using individual records for the first time in group-housed rabbits, we show that variables defining how resources are distributed among cage mates as well as an animal's priority for access to feed can be good indicators of the animal's dominance/subordination position within the cage. The most efficient animals are the ones that eat fewer times, consume less amount of feed and spend less time in the feeder through. They also appear to be the subordinates, as evidenced by the fact that they do not have priority access to feed and have the smallest share of resources.

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2024.101090.

Ethics approval

Not applicable.

Data and model availability statement

The data/models were not deposited in an official repository, but they are available from the authors upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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M. Piles: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **M. Mora:** Writing – review & editing, Methodology, Investigation, Formal analysis. **I. Kyriazakis:** Writing – review & editing, Methodology. **L. Tusell:** Writing – review & editing, Investigation. **M. Pascual:** Writing – review & editing, Investigation. **J.P. Sánchez:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of interest

The authors declare that they have no competing interests.

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