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A meta-analysis on the effects of the housing environment on the behaviour, mortality, and performance of growing rabbits

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Abstract

*Although the number of rabbits (*Oryctolagus cuniculus*) produced in Europe is important, they are under-represented in welfare research. Studies on the effects of housing conditions have focused on performance and mortality. We conducted a meta-analysis to further understand the impact of the housing environment on growing rabbits. Whilst providing a robust quantifiable review, meta-analyses are restricted to existing literature. We included information on behaviour, mortality and performance. Twenty-seven peer-reviewed and conference publications, with a total of 99 experimental treatments, were used. We collected information about rabbit age, bodyweight, sex and breed; allometric space allowance, pen height, group size, environmental temperature, floor type, substrate and enrichment use, lighting, diet and medicated feed. Predictive equations for each response variable were calculated using multiple regression models. Higher space allowance was found to increase locomotor and social activity, and to reduce resting and comfort behaviour. Restricted pen height increased ingestive behaviour; comfort behaviours decreased as space allowance increased, although these might have been confounded with self-directed behaviours in literature. Mortality remained stable at varying space allowances, but increased with larger group sizes and enrichment objects. Growth rate, feed intake and feed conversion were reduced with higher space allowances and larger group sizes, and by provision of substrate and enrichment objects. Findings suggest that higher space allowance and unrestricted pen height are beneficial for rabbit behaviour, but might have undesired consequences if considered independent from other aspects. The challenge of promoting welfare in commercial conditions was highlighted, as a number of parameters which improved behavioural expression reduced performance. In certain cases welfare inputs complemented performance, including providing non-medicated feed and higher space allowance in cooler climates. Although our results should be interpreted with caution given the limitations of the included variables, they are expected to contribute to the improvement of current and new rabbit housing systems to optimise welfare.*

Keywords: *animal welfare, behaviour, growing rabbit, meta-analysis, mortality, performance*

Introduction

Literature on the effects of housing conditions on farmed growing rabbits (*Oryctolagus cuniculus*) is relatively small as compared to other farmed species, despite almost one billion rabbits being reared during 2013. Most production (about 230 million rabbits and hares [genus *Lepus*]) is based in China, although Europe produced about 107 million rabbits during 2013, where they are, in terms of total number produced, one of the most important farmed animal species (FAOSTAT 2013). Growing rabbit production systems mostly consist of conventional cages, and no general legal framework exists in the European Union (EU) regarding rabbit protection. Several European countries have taken individual initiatives and adopted minimum legal welfare requirements (The Netherlands, Germany, Austria, Switzerland and Belgium). Legal restrictions should be objectively based but, as reported by the European Food and Safety Authority (EFSA 2005) and suggested by several authors (Mirabito 2007; Szendrő & Dalle Zotte 2011), little research has been conducted on how farming conditions affect growing rabbits as compared to other species, which translates into knowledge gaps that make political decisions difficult.

As indicated by the EFSA (2005), some aspects characterising most current intensive housing systems do not meet rabbits' biological needs. Specific concerns are space allowance, enrichment, mortality and restricted behavioural expression (Dixon *et al* 2010; Buijs *et al* 2011), which span the biological, natural and feeling-based components defining animal welfare (Fraser 2003). Space allowance is a key issue, as rabbits may experience severe space restriction in small cages. Nevertheless, current information may be misleading, since space allowance is usually expressed as rabbits per area unit, not considering changes in bodyweight as they grow (Petherick & Phillips 2009). Group size also requires further attention, since growing rabbits are kept in variable group sizes. As a social species, individual housing is stressful (Podberseck *et al* 1991; Gunn & Morton 1995), but large groups might also result in compromised health or limited access to resources, particularly when space is limited (Estevez *et al* 2007). As a recently domesticated species, rabbits behave similarly to their wild counterparts with slight changes in the frequency and intensity of certain behaviours (Trocino & Xiccato 2006). Enrichment is not provided in conventional cages, resulting in barren environments often lacking stimulation (EFSA 2005). In recently developed alternative indoor systems, rabbits are provided with tubes, platforms, gnawing blocks and hay dispensers (Maertens *et al* 2004; BAWC 2012). Enrichment should be biologically meaningful to the animal (Newberry 1995), and therefore information about the true benefits of enrichment for rabbits is still necessary. Performance should also be considered, as stressful conditions are known to affect animals' feed intake and growth (Moberg 2000) and welfare improvements may be difficult to adopt if they have an associated negative economic impact.

Meta-analyses are systematic approaches to literature that, beyond classical reviews, allow quantitative summarising of results from multiple studies. They are ranked highly as a form of evidence (Petrie & Watson 2006), and are widely used in medical and psychological sciences, providing an objective appraisal and accurate estimate of common treatment effects (Egger *et al* 1997) to support decisions on evidence-based policy and practice (Borenstein *et al* 2009). To date, meta-analyses have been published on dog cognition and personality (Dorey *et al* 2009; Fratkin *et al* 2013) and stereotypy in zoo animals (Shyne 2006). Meta-analytical techniques have also been applied to examine the effect of housing systems on growing-finishing pigs (*Sus scrofa*) (Averós *et al* 2010a,b, 2012; Douglas *et al* 2015) and gestating sows (Douglas *et al* 2014), providing useful guidance towards improvement of production systems. The manner in which housing elements interact and affect rabbits requires further attention, and so the use of a meta-analytical approach might contribute to gaining new research perspectives and guidance on management practices and improved welfare standards.

The aim of this study was to quantify the effects of allometric space allowance, group size, use of substrate and enrichment on the behaviour, mortality, and performance of growing rabbits.

Materials and methods

The methodology is based on St-Pierre (2001) and Sauvant *et al* (2008), and followed the steps described by Hamer and Simpson (2002). This method has been successfully used in studies such as Averós *et al* (2010a,b, 2012) and Douglas *et al* (2014, 2015).

Data collection

Information regarding the effects of the physical environment and animal traits on behaviour, mortality and performance of growing rabbits was collected from studies published in peer-reviewed journals and conference proceedings between 1975 and 2014. Our main interest was the effects of space allowance, group size, use of environmental enrichment and substrate, and studies testing these effects were the main literature search focus, which was carried out using the ISI Web of Knowledge and Science Direct online databases. Combinations of terms 'rabbit' and 'space allowance', 'density', 'group size', 'enrichment', 'bedding' 'welfare', 'behaviour', or 'performance' were used. References relative to growing rabbits were retained, with studies on laboratory rabbits being only retained if they tested the effect of the physical environment on any of the response variables and did not involve medical procedures. References of retained papers were also checked for completeness.

The first literature search resulted in 161 candidate papers which underwent a second review. For inclusion in the database, papers had to report for each experimental treatment (or time interval within experimental treatment) information about: (i) sex, genetics, initial/final age, and initial/final bodyweight (BW); (ii) space allowance, group size, average environmental temperature, floor characteristics, presence of substrate, use of enrichment objects, pen height restriction, and light characteristics; (iii) diet's crude protein (CP) content (given its implications for performance and feeding behaviour) and use of medicated feed (either antibiotic and/or coccidiostat); (iv) replicates per treatment (ie units to which an experimental treatment was applied), duration of the experimental period (or time interval within the experimental period in case of repeated measures), and duration of observation periods for behaviours; (v) behaviour, mortality and/or performance as dependent variables (information on at least one dependent variable). Papers reporting the use of enrichment sources promoting the environmental complexity and/or rabbit's physical activity (platforms and physical barriers) were discarded due to the limited number of papers fulfilling requirements. Only papers reporting the use of enrichment objects were therefore used. Similarly, use of crude fibre content was discarded due to the limited amount of homogenously reported information.

A total of 27 manuscripts and experiments, 99 experimental treatments and 262 observations (within one experimental period, a paper may report information about either one or several time intervals) were finally available for database inclusion and analysis (Table 1). An Excel® database was built, and each experiment uniquely identified. We recorded independent and response variables associated with each observation (each treatment over the whole experimental period, or each treatment within each time interval in case of repeated measures). For each treatment, the duration of the experimental period/time interval was collected. When repeated measures were provided at different time intervals over the whole experimental period, values for response variables at the end of each time interval were used. The number of replicates per treatment was collected, as well as the duration of behaviour recording periods.

For each experimental treatment sex (male/female/mixed) was collected; 'mixed' for housing or reporting results of both sexes together. New Zealand White and Pannon White breeds were identified separately, while hybrids and other less-frequent breeds were pooled together. Initial/final age and BW were also collected. Since spatial needs of growing animals change with time (Petherick & Phillips 2009) space allowance was expressed in allometric terms (*k*-value; $cm^2/g^{0.667}$) at the end of each experimental period/time interval. Group size (number of rabbits), average environmental temperature during each experimental period (ºC), floor characteristics (discontinuous/continuous flooring), use of substrate (not used/as feed/as bedding), pen height restriction (yes/no), presence of enrichment objects (yes/no), light characteristics (natural/artificial/artificial with dawn-dusk periods), diet protein content (%), and use of medicated feed (yes/no) were also collected. Due to limited information, wired and plastic slatted floors were pooled together as 'discontinuous flooring'. A wired floor totally covered with bedding was considered 'continuous flooring'.

Response variables were grouped into behaviour, mortality and performance categories, and each manuscript was used to obtain one or several models, depending on the reported information. Behaviour was based on time budgets (frequency of each behaviour/observation period; %). The ethogram, based on Gunn and Morton (1995), consisted of: comfort behaviour (grooming, scratching and washing), ingestive behaviour (eating and drinking), locomotor behaviour (walking/running and hopping), resting behaviour (sleeping, lying down, sitting and rearing), and social interactions (sniffing, nosing, grooming or biting other rabbits). Exploratory behaviours were discarded due to limited information available. Mortality was expressed as % of dead/culled rabbits at the end of the experimental period/time interval. Performance variables included average daily gain (ADG; g per day), average daily feed intake (ADFI; g per day), and feed conversion ratio (FCR; ADFI per ADG). Variables were either directly collected from manuscripts, or estimated using available information whenever possible. A descriptive summary of variables is provided in Table 2.

Table 1 Studies included in the meta-analysis of the effects of the physical environment and animal characteristics on the welfare of growing rabbits.

Paper	Behaviour	Mortality	Performance
Matics *et al* (2014)		X	X
Volek *et al* (2014)			X
Abdelfattah *et al* (2013)	X		X
Trocino *et al* (2013)	X		X
Xiccato *et al* (2013a)		X	X
Xiccato *et al* (2013b)			X
Szendro *et al* (2012)	X	X	X
Zucca *et al* (2012)	X		X
Jekkel *et al* (2010)	X		X
Gondret *et al* (2009)		X	X
Lazzaroni *et al* (2009)			X
Princz *et al* (2009)		X	X
Szendro *et al* (2009)			X
Jordan *et al* (2008)		X	X
Princz *et al* (2008a)			X
Princz *et al* (2008b)		X	X
Princz *et al* (2008c)	X		X
Onbasilar and Onbasilar (2007)			X
Tuyttens *et al* (2005)		X	X
Salcedo-Baca *et al* (2004)		X	X
McNitt *et al* (2003)		X	X
Dal Bosco *et al* (2002)	X	X	X
Maertens and Van Herck (2000)		X	X
Morisse *et al* (1999)	X		
Chiericato *et al* (1996)		X	X
Maertens and De Groote (1985)		X	X
Maertens and De Groote (1984)		X	X

Statistical analysis

Predictive equations for each response variable were calculated using multiple regression, generalised linear mixed models (GLIMMIX procedure; SAS 2011). Due to differences in the nature and availability of information, models differed according to the group of variables.

Behaviour

Information was more limited, and behaviour models were simpler. Main fixed effects included: (i) sex (male vs female vs mixed); (ii) dietary CP content (%, as-fed basis); (iii) average temperature (ºC) during the experimental period; (iv) space allowance (*k*-value, $cm^2/g^{0.667}$) at the end of the experimental period, and its quadratic term to account for any plateau effect; (v) group size (n) and its quadratic term to account for any plateau effect; floor characteristics (discontinuous vs continuous); (vi) use of bedding substrate (yes vs no); (vii) use of enrichment objects (presence vs absence); (viii) pen height restriction (yes vs no); and (xi) use of medicated diet (yes vs no). The quadratic term of *k*-value was significant for most behaviours ($P < 0.05$) and was retained in all models. The opposite was detected for the quadratic term of group size, which was removed from models. Initial age (days) at the beginning of experimental period, duration of experimental period (days), and duration of behavioural observations (h) were also included in models as covariates. The individual experiment and moment of observation during the experi-

Table 2 Descriptive statistics for the continuous independent and dependent variables, and covariates included in the models.

Variable	n	Minimum	Maximum	Mean (± SD)	Median
Continuous variables					
k-value (cm^2/g$^{0.667}$)	262	1.7	18.1	5.4 (± 4.6)	2.5
Group size (n)	262	1	34	9.0 (± 7.1)	8
Average temperature (°C)	262	11.3	26.3	18.3 (± 2.1)	18
CP (%, as fed)	262	14.4	20.9	15.7 (± 1.3)	15.9
Covariates					
Initial age (days)	262	27	70	47.2 (± 12.7)	43
Duration of experimental period (days)	262	7	62	20.9 (± 17.2)	7
Duration of behaviour recording (h)	55	0.17	24	15.8 (± 11.4)	24
Continuous variables					
Resting behaviours (% of time)	55	12.0	79.9	59.3 (± 14.7)	62.9
Locomotor behaviours (% of time)	55	0.5	19.4	7.8 (± 5.7)	6.1
Ingestive behaviours (% of time)	45	3.0	16	11.3 (± 2.8)	11.8
Comfort behaviours (% of time)	49	3.0	21.8	11.2 (± 4.9)	11.2
Social behaviours (% of time)	49	0	8.1	2.9 (± 2.4)	1.7
Mortality (%)	136	0	25	3.0 (± 4.5)	1.4
ADG (g per day)	258	19	52.7	38.5 (± 5.8)	39.7
ADFI (g per day)	252	54.7	186	125.9 (± 24.9)	129.8
FCR	252	1.7	6.4	3.3 (± 0.8)	3.2

n = total number of observations for which the information is available; CP = crude protein; ADG = average daily gain; ADFI = average daily feed intake; FCR = feed conversion ratio.

ment, nested within experiment, were included as random factors (St-Pierre 2001; Sauvant *et al* 2008). Weighting observations is advisable to account for inter-experiment variance heterogeneity (Sauvant *et al* 2008), but is not always feasible due to a lack of homogeneity across papers in reporting variability. To overcome the problem, sample size was proposed as an indirect variance estimate (Lipsey & Wilson 2000). In our case this is the group size (number of rabbits per experimental unit), which was already included. Although unweighted observations have also been used (see Schmidely *et al* 2008) number of replicates per treatment, as a measure of each experiment's statistical power (Thomas & Juanes 1996), was used as the weighting criterion of each observation.

Initial models included all fixed effects and two-way interactions. Final models were calculated using a stepwise backwards procedure, in which non-significant interactions were gradually removed from models using the highest *P*-value as the criterion. Final models retained significant interactions ($P < 0.05$) and those showing a statistical trend ($P < 0.10$). Root mean square errors (RMSE) were calculated as an estimate of models' prediction accuracy.

Mortality and performance

For mortality, ADG, ADFI and FCR main fixed effects were: (i) sex (male vs female vs mixed); (ii) genetics (New Zealand White vs Pannon White vs Other breeds/hybrids); (iii) dietary CP content (%, as-fed basis); (iv) average temperature (ºC) during the experimental period; (v) space allowance (*k*-value, cm^2/g$^{0.667}$), and its quadratic term at the end of the experimental period when statistically significant ($P < 0.05$); (vi) group size (n), and its quadratic term when statistically significant ($P < 0.05$); floor characteristics (discontinuous vs continuous); (vii) use of substrate (no substrate vs as feed vs as bedding); (viii) use of enrichment objects (presence vs absence); (ix) pen height restriction (yes vs no); (x) light characteristics (natural vs artificial vs artificial with dawn-dusk periods); and (xi) use of medicated diet (yes vs no). Rabbits' initial age (days) and experimental period duration (days) were also included as covariates. The experiment and time of observation, nested within experiment, were included as random factors. Number of replicates per treatment was also used to weight observations. Final models were obtained as previously described.

Table 3 Parameter estimates (SE) for the models quantifying the effect of the different factors on the resting, locomotor, and ingestive behaviour of growing rabbits.

Variable		Resting (%; n = 55)	*P*-value	Locomotor (%; n = 55)	*P*-value	Ingestive (%; n = 45)	*P*-value
Intercept		–677.19 (286.27)	0.099	–38.62 (57.36)	0.549	–4.62 (46.00)	0.936
Behaviour observation time		4.36 (1.97)	0.033	–0.37 (0.34)	0.281	0.08 (0.34)	0.812
Experimental days		1.95 (0.86)	0.029	0.26 (0.16)	0.107	0.09 (0.16)	0.558
Initial age		–0.67 (0.19)	0.001	0.02 (0.06)	0.708	–0.20 (0.06)	0.003
Sex	Males	–1.38 (6.22)	0.957	–0.02 (3.02)	0.990	–0.18 (2.73)	0.926
	Females	0.39 (6.23)		–0.40 (3.00)		0.83 (2.74)	
	Mixed	0		0		0	
Medicated diet	No	–5.16 (17.45)	0.769	2.56 (1.09)	0.025	2.36 (2.17)	0.286
	Yes	0		0		0	
CP		49.31 (18.36)	0.011	–1.56 (2.77)	0.579	1.64 (2.52)	0.520
Average temperature		–8.82 (5.32)	0.106	3.83 (1.23)	0.004	–0.50 (0.66)	0.455
k-value		2.78 (1.59)	0.089	7.64 (3.25)	0.025	0.75 (0.56)	0.190
k-value × *k*-value		–0.40 (0.12)	0.001	0.34 (0.09)	0.001	–0.08 (0.04)	0.050
Group size		–0.36 (0.23)	0.126	0.11 (0.08)	0.199	–0.02 (0.10)	0.824
Enrichment	No	1.07 (2.22)	0.634	–0.19 (1.16)	0.872	0.77 (1.22)	0.535
	Yes	0		0		0	
Substrate	No	0.08 (3.54)	0.983	0.60 (1.83)	0.744	0.20 (2.53)	0.936
	Yes	0		0		0	
Unrestricted height	No	–3.39 (2.58)	0.197	0.65 (1.23)	0.600	2.13 (1.10)	0.064
	Yes	0		0		0	
Discontinuous flooring	No	1.51 (2.10)	0.475	–0.78 (1.03)	0.454	–0.54 (0.91)	0.557
	Yes	0		0		0	
k-value × average temperature				–0.58 (0.20)	0.008		
RMSE		0.53		0.32		0.29	

CP = crude protein; RMSE = root mean square error of the model.

Results

Behaviour

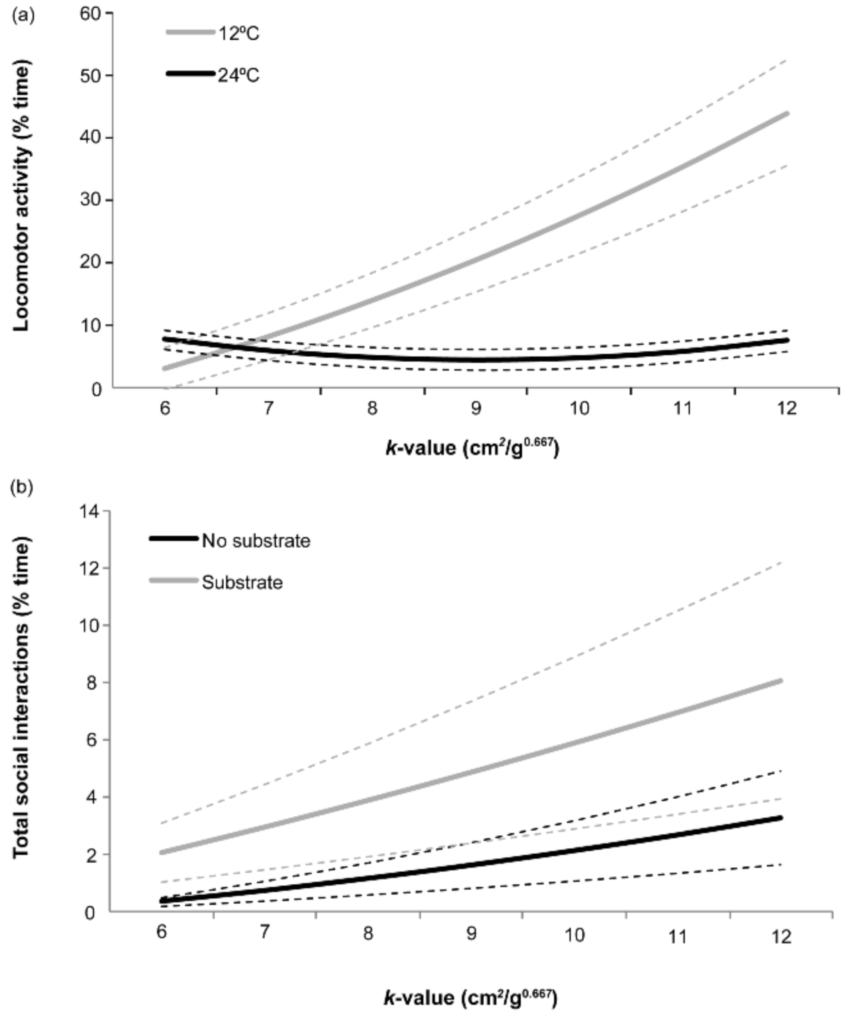
Resting behaviour (RMSE = 0.53; Table 3) was predicted to increase with observation time and experimental period durations ($P < 0.05$) and to decrease with initial age ($P < 0.01$). It also increased with dietary CP content ($P < 0.05$), and tended to decrease as space allowance increased, with a negative coefficient found for its quadratic term ($P < 0.01$). Locomotor activity (RMSE = 0.32) was higher with non-medicated feed ($P < 0.05$), and was predicted to remain almost invariable at high temperatures, but to increase with increasing space at relatively low temperatures ($P < 0.01$; Figure 1[a]). Ingestive activities (RMSE = 0.29) decreased with initial age ($P < 0.01$), tended to be negatively correlated to the quadratic term of *k*-value ($P < 0.10$) and to be higher with pen height restriction ($P < 0.10$).

Comfort behaviours (RMSE = 0.16) decreased as the experimental period increased ($P < 0.01$; Table 4), and increased with initial age ($P < 0.001$). They decreased as space allowance increased ($P < 0.01$), and a positive coefficient was found for its quadratic term ($P < 0.001$). Comfort behaviours were less frequent on continuous flooring ($P < 0.05$). Social behaviours (RMSE = 0.11) were more frequent as rabbits grew older ($P < 0.01$) and decreased with diet CP content ($P < 0.05$). Their frequency was higher when enrichment objects were absent ($P < 0.05$), and tended to be smaller with restricted height ($P < 0.10$). Frequency of social behaviours increased with space allowance, particularly with substrate ($P < 0.01$; Figure 1[b]).

Mortality

Mortality increased with initial age (RMSE = 0.20; $P < 0.01$; Table 5) and was predicted to remain low and

Figure 1



Predicted effect (standard error of prediction in dotted lines) of the interaction between (a) space allowance and the average temperature on the locomotor activity and (b) between space allowance and the use of substrate on the social interactions of growing rabbits (for the median of the other continuous independent variables and covariates).

stable when enrichment objects were absent, but to increase with space allowance when enrichment objects were present ($P < 0.01$; Figure 2[a]). Mortality increased with group size, the increase being particularly apparent in the absence of enrichment objects ($P < 0.01$; Figure 2[b]).

Performance

Average daily gain (RMSE = 0.24; Table 6) decreased as initial age ($P < 0.001$), CP ($P < 0.05$) and average temperature ($P < 0.001$) increased. Lowest ADG was predicted when substrate was provided as feed ($P < 0.01$), followed by substrate provided as bedding and by no bedding. An overall ADG decrease was predicted as space allowance increased, but the decrease rate was faster as group size grew larger ($P < 0.001$; Figure 3[a]). The ADG decrease as space allowance increased was particularly apparent in presence of enrichment objects ($P < 0.001$; Figure 3[b]).

Average daily feed intake increased with experimental period duration (RMSE = 0.69; $P < 0.001$) and initial age ($P < 0.001$), and decreased as average temperature increased ($P < 0.001$). Predicted ADFI was lowest when substrate was provided as feed, followed by provision as bedding and by substrate absence ($P < 0.05$). Interaction between space allowance and group size on ADFI showed a similar pattern to that described for ADG ($P < 0.001$; Figure 4[a]), similar to the interaction between space allowance and enrichment object use ($P < 0.001$; Figure 4[b]). A slight decrease in ADFI was predicted as group size increased with restricted pen height, with the opposite for unrestricted height ($P < 0.05$; Figure 4[c]).

Feed conversion ratio increased with experiment duration (RMSE = 0.02; $P < 0.05$) and initial age ($P < 0.001$), and was smaller with non-medicated feed ($P < 0.05$). Similarly to ADG and ADFI, FCR increased with increasing space allowance, with rate being faster as group size was larger ($P < 0.001$; Figure 5[a]). At low temperature FCR decreased when space allowance increased, and increased with space allowance at high temperature ($P < 0.01$; Figure 5[b]).

Table 4 Parameter estimates (SE) for the models quantifying the effect of the different factors on the comfort and social behaviour of growing rabbits.

Variable		Comfort		Social	
		(%; n = 49)	*P*-value	(%; n = 49)	*P*-value
Intercept		151.50 (78.54)	0.194	83.60 (33.22)	0.128
Behaviour observation time		–0.51 (0.56)	0.364	–0.41 (0.26)	0.115
Experimental days		–0.88 (0.27)	0.003	–0.07 (0.08)	0.365
Initial age		0.31 (0.08)	< 0.001	0.09 (0.03)	0.003
Sex	Males	–0.61 (1.57)	0.900	–0.02 (1.31)	0.837
	Females	0.03 (1.57)		–0.69 (1.30)	
	Mixed	0		0	
Medicated diet	No	–8.78 (5.90)	0.147	0.49 (2.62)	0.854
	Yes	0		0	
CP		–7.13 (4.99)	0.163	–5.42 (2.19)	0.019
Average temperature		0.79 (1.41)	0.581	0.34 (0.68)	0.618
k-value		–3.15 (0.95)	0.002	0.62 (0.57)	0.526
k-value × *k*-value		0.25 (0.05)	< 0.001	0.02 (0.02)	0.316
Group size		0.07 (0.07)	0.311	0.09 (0.06)	0.128
Enrichment	No	–0.22 (0.56)	0.694	1.06 (0.47)	0.030
	Yes	0		0	
Substrate	No	0.88 (0.84)	0.303	1.35 (1.19)	0.266
	Yes	0		0	
Unrestricted height	No	–1.09 (1.03)	0.296	1.65 (0.86)	0.064
	Yes	0		0	
Discontinuous flooring	No	–0.91 (0.44)	0.046	0.08 (0.51)	0.875
	Yes	0		0	
k-value × substrate	No			–0.51 (0.16)	0.004
	Yes				
RMSE		0.16		0.32	

CP = crude protein; RMSE = root mean square error of the model.

Discussion

We quantified the effects of aspects characterising all production systems on the behaviour, mortality, and performance of growing rabbits. Given their implications, we focused on space allowance, group size, use of substrate and enrichment objects (Szendrő & Luzi 2006; Verga *et al* 2007), but other aspects were also considered. Interpretation of results should be limited to the boundaries of ranges of values shown in Table 2. We acknowledge that the amount of papers used was limited, but this is due to restrictions regarding the information that candidate papers contained. Despite this, information of the present study is, in our view, still extremely valuable, and could be enlarged once new manuscripts are available.

Space allowance

Literature has emphasised the relevance of space allowance for farm species, as well as its confusion with group size (Estevez *et al* 2007), the latter aspect, as suggested by Buijs *et al* (2011), being particularly relevant in rabbit studies. We determined the interactive effect of space allowance and group size on growing rabbits, and used allometric measures of space allowance as this is the most suitable approach for growing animals (Petherick & Phillips 2009). We found very small changes in the percentage of time spent at feeders as space allowance increased, but a significant decrease in ADFI. This can be explained by the fact that reduced space allowance is stressful for rabbits and increases feed wastage (Mbanya *et al* 2004), so that some

Table 5 Parameter estimates (SE) for the models quantifying the effect of the different factors on the mortality of growing rabbits.

Variable		Mortality (%; n = 136)	*P*-value
Intercept		47.69 (52.25)	0.380
Experimental days		–0.02 (0.26)	0.949
Initial age		0.12 (0.04)	0.006
Breed	NZW	–0.20 (1.21)	0.722
	PW	–7.24 (9.07)	
	Others	0	
Sex	Males	1.66 (3.32)	0.104
	Females	7.28 (3.47)	
	Mixed	0	
Medicated diet	No	5.57 (4.61)	0.230
	Yes	0	
CP		–3.01 (3.06)	0.329
Average temperature		–0.01 (0.08)	0.912
k-value		1.80 (0.65)	0.019
Group size		–0.66 (0.27)	0.071
Group size × Group size		0.02 (0.01)	0.025
Enrichment	No	1.52 (4.07)	0.710
	Yes	0	
Substrate	No	1.97 (1.81)	0.549
	For feed	2.93 (6.55)	
	For bedding	0	
Unrestricted height	No	1.10 (1.23)	0.374
	Yes	0	
Discontinuous flooring	No	–0.32 (1.29)	0.803
	Yes	0	
Light type	Artificial	–5.40 (13.29)	0.921
	Natural	–6.00 (16.09)	
	Artificial with dawn-dusk periods	0	
k-value × enrichment	No	–1.64 (0.60)	0.008
	Yes	0	
Group size × enrichment	No	0.51 (0.17)	0.004
RMSE		0.20	

NZW = New Zealand White; PW = Pannon White; CP = crude protein; RMSE = root mean square error of the model.

feeder visits might be a form of behavioural redirection to fight stress. This could also explain why pen height restriction, which is known to be detrimental for rabbits (Morton *et al* 1993; Hansen & Berthelsen 2000), also tended to increase time spent at feeders.

Spatial restriction limits rabbits' behavioural repertoire (Verga *et al* 2007), and increased activity levels might be expected at high space allowance. An overall reduction in resting time was found at higher space allowances, in accordance with Buijs *et al* (2011), who observed a decrease in sternal lying as space allowance increased, and with findings for growing pigs (Averós *et al* 2010b). A simultaneous increase in locomotor activity was also found, suggesting that reducing space limitation encourages movement of rabbits around the pen, although this occurred only at relatively low temperature (Figure 1[a]). Rabbits' comfort zone is around 21ºC (Fayez *et al* 1994), and locomotion was predicted to remain low and invariable at hotter temperatures, likely reflecting behavioural adaptations to maximise heat loss (Lebas *et al* 1997). Effects of increased space allowance on rabbit movement would therefore be modulated by other aspects, such as environmental temperature.

Comfort behaviours were predicted to decrease as space allowance increased, which appears to contradict previous findings. An explanation could be that grooming or washing might have been confounded with self-directed behaviours in some of the papers used, as Gunn and Morton (1995) observed that rabbits performed stereotypies in between grooming bouts, making distinction difficult. Self-directed behaviours can reflect a negative emotional state (Hess 2004), and should be more frequent at reduced space allowance. This would explain why comfort behaviours were high at a reduced space allowance, decreasing when more space is given. Higher space and presence of substrate also resulted in more social interactions (Figure 1[b]), but this should be interpreted carefully since separate models for positive and negative social interactions could not be obtained and increased space allowance, although generally positive, may also have undesired effects. For instance, in broiler chickens, aggressive encounters were observed more frequently at moderately crowded levels, and mainly occurred in open spaces (Pettit-Riley *et al* 2002). All social behaviours also tended to be more frequent with restricted pen height.

In their review, Szendrő and Dalle Zotte (2011) reported a detrimental effect of reduced space allowance and large group size on rabbits' performance, but failed to provide an overall picture of the effect of space allowance on rabbit growth because of the variability of studies using intermediate space allowances. This might be attributed to differences in BW across studies, and the fact that changes in spatial needs as rabbits grow were not considered, as already suggested (Maertens & De Groote 1985; Aubret & Duperray 1992). Using allometry, we found an

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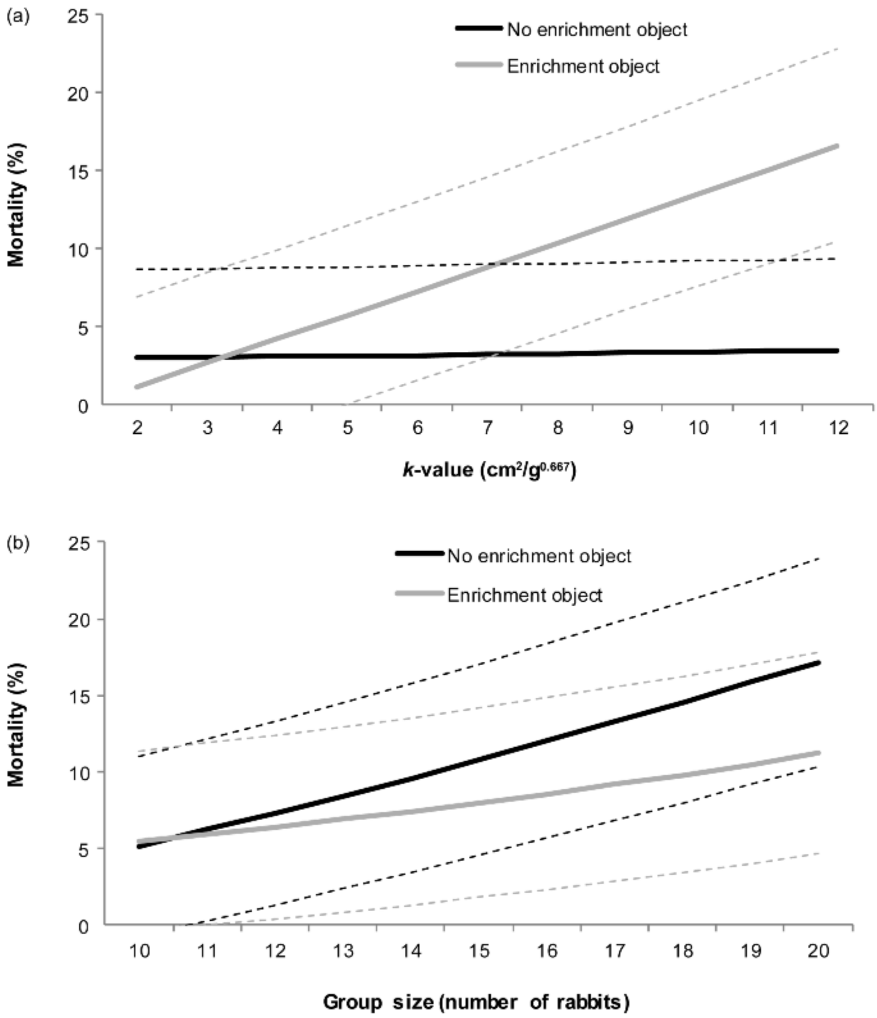
Figure 2



Predicted effect (standard error of prediction in dotted lines) of the interaction between (a) space allowance and the use of enrichment object, and (b) group size and the use of enrichment object, on the mortality of growing rabbits (for the median of the other continuous independent variables and covariates).

overall decrease in ADG and ADFI as rabbits had more space, an effect even more apparent in larger groups. This might be due to increased activity levels, as previously suggested (Verga *et al* 2007), and to the fact that by combining large space allowance and larger group sizes, the total effective space becomes even larger (McGlone & Newby 1994). Reduction in ADFI would be the result of the described feed spillage reduction. Higher space allowance resulted in increased FCR, particularly with larger group sizes, likely due to increased activity resulting in higher energy expenditure. Increased activity may generally be interpreted as positive for welfare although, as mentioned, may have undesired implications. Producers would additionally be unwilling to provide more space if this reduces their sale value or increases the feeding costs per product unit. Marketing products at increased retail prices is a solution adopted by some businesses with improved welfare standards (Fulponi 2006).

Group size

No effect of group size was found on behaviour, as observed for growing pigs (Averós *et al* 2010a,b, 2012). Since it is known that large group sizes can lead to increased aggression at restricted space allowance (Estevez *et al* 2007), the fact that total social interactions remained invariable as group size changed suggests that, at least in some of the studied papers, effects originally attributed to larger group sizes were actually caused by reduced space allowance, which acted as a confounding effect. Space allowance therefore appears more relevant for rabbit behaviour than group size, although the effect of the latter cannot be neglected. We found that, for a given space allowance and independent from enrichment objects, mortality overall increases at larger group sizes (Figure 2[b]), but Verga *et al* (2007) suggested that it is the crowding associated with larger group size that increases rabbit mortality. This highlights again the confusion between space allowance and

Table 6 Parameter estimates (SE) for the models quantifying the effect of the different factors on the performance of growing rabbits.

Variable		ADG (g per day; n = 258)	P-value	ADFI (g per day; n = 252)	P-value	FCR (ADFI/ADG; n = 252)	P-value
Intercept		84.91 (13.81)	< 0.001	183.54 (69.55)	0.016	2.124 (2.045)	0.311
Experimental days		–0.08 (0.06)	0.237	0.94 (0.27)	< 0.001	0.015 (0.007)	0.036
Initial age		–0.20 (0.03)	< 0.001	1.95 (0.08)	< 0.001	0.068 (0.002)	< 0.001
Breed	NZW	–1.11 (2.44)	0.696	2.98 (4.79)	0.501	0.080 (0.138)	0.403
	PW	–1.34 (2.71)		–12.45 (12.96)		–0.392 (0.334)	
	Others	0		0		0	
Sex	Males	–2.56 (2.44)	0.390	–3.00 (9.59)	0.902	0.092 (0.259)	0.933
	Females	–3.49 (2.71)		–4.55 (10.02)		0.084 (0.274)	
	Mixed	0		0		0	
Medicated diet	No	1.54 (1.32)	0.247	–4.75 (6.32)	0.453	–0.331 (0.161)	0.041
	Yes	0		0		0	
CP		–1.68 (0.81)	0.038	–5.49 (4.09)	0.181	0.092 (0.106)	0.383
Average temperature		–0.51 (0.11)	< 0.001	–3.90 (0.32)	< 0.001	–0.190 (0.043)	< 0.001
k-value		–0.01 (0.79)	0.988	–4.64 (1.72)	0.058	–0.425 (0.137)	0.002
k-value × *k*-value		–0.08 (0.03)	0.010				
Group size		0.93 (0.17)	< 0.001	2.13 (0.58)	0.002	–0.042 (0.013)	0.001
Enrichment	No	–8.14 (2.26)	< 0.001	–20.60 (7.10)	0.004	0.070 (0.059)	0.234
	Yes	0		0		0	
Substrate	No	2.05 (1.95)	0.002	10.05 (6.19)	0.025	–0.025 (0.148)	0.453
	For feed	–16.40 (5.76)		–29.62 (18.51)		0.604 (0.520)	
	For bedding	0		0		0	
Unrestricted height	No	0.09 (0.87)	0.915	9.08 (4.64)	0.052	–0.070 (0.063)	0.270
	Yes	0		0		0	
Discontinuous flooring	No	–0.42 (0.82)	0.608	–1.40 (2.75)	0.612	–0.075 (0.060)	0.218
	Yes	0		0		0	
Light type	Artificial	1.80 (4.74)	0.391	0.53 (22.76)	0.871	0.342 (0.576)	0.261
	Natural	4.74 (4.94)		–5.48 (23.92)		–0.130 (0.607)	
	ADDP	0		0		0	
k-value × group size		–0.24 (0.04)	< 0.001	–0.36 (0.11)	< 0.001	0.010 (0.003)	< 0.001
k-value × average temperature						0.022 (0.007)	0.003
k-value × enrichment	No	1.86 (0.50)	< 0.001	5.35 (1.57)	< 0.001		
	Yes	0		0			
Group size × unrestricted height	No			–1.12 (0.44)	0.012		
	Yes			0			
RMSE		0.24		0.69		0.02	

ADG = average daily gain; ADFI = average daily feed intake; FCR = feed conversion ratio; NZW = New Zealand White; PW = Pannon White; CP = crude protein; ADDP = artificial with dawn-dusk periods; RMSE = root mean square error of the model.

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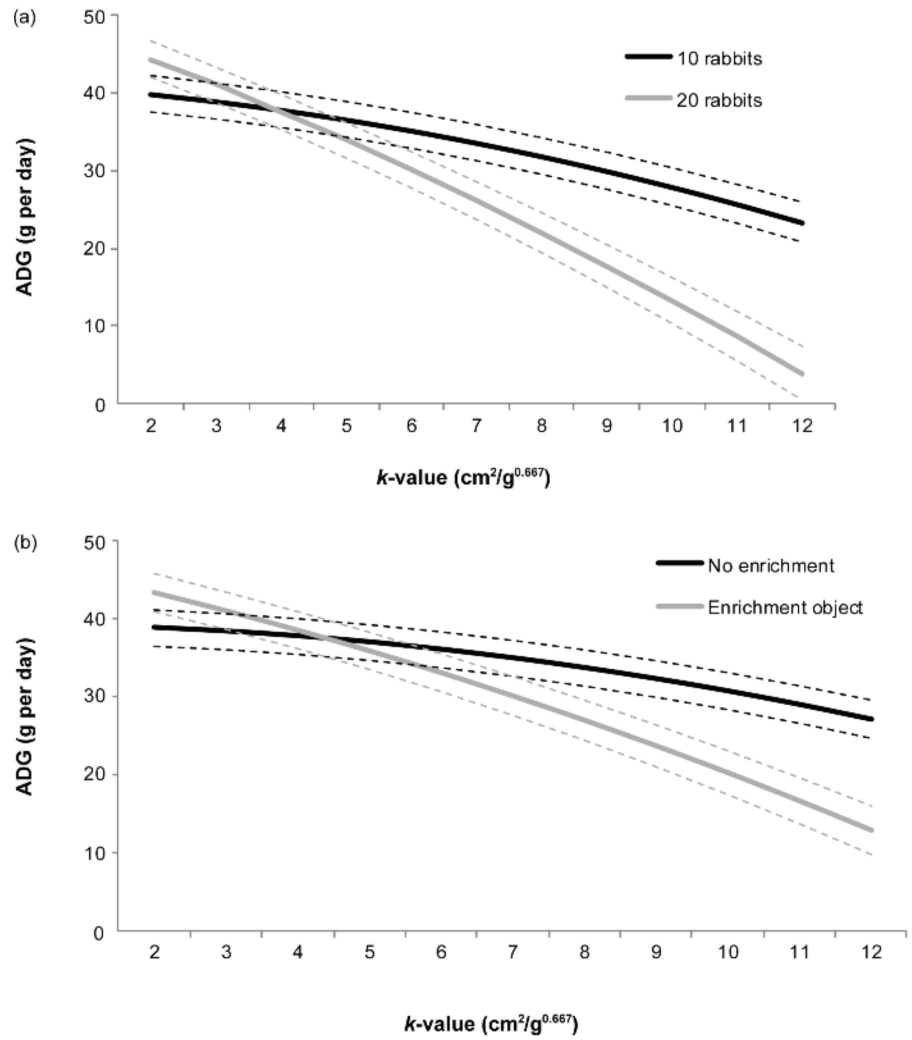
Figure 3



Predicted effect (standard error of prediction in dotted lines) of the interaction between (a) space allowance and group size and (b) space allowance and the use of enrichment object, on the ADG of growing rabbits (for the median of the other continuous independent variables and covariates). ADG = average daily gain.

group size. Therefore, in order to set an adequate group size, certain other factors have also to be considered, such as enough space allowance, availability of enrichment objects, and environmental temperature.

Use of enrichment and substrate

Social behaviours were less frequent when enrichment objects were present (Table 4), similar to that observed by Buijs *et al* (2011). Barren conditions result in inactivity, boredom, frustration (Huls *et al* 1991; Morton *et al* 1993), and in behavioural redirection towards other rabbits, as described in pigs (Fraser *et al* 1991), and our results would confirm this. Surprisingly, increased mortality was predicted at higher space allowance when enrichment objects were present, but this would be linked to the nature and number of these objects. High space allowance promotes activity, and this likely led to more frequent interactions with enrichment objects. It is difficult to maintain adequate hygiene of these objects, and the number of objects used in studied papers was probably insufficient for the group sizes, which would have resulted in competition for them and social disturbance (Buijs *et al* 2011), as described for pigs (Van de Weerd & Day 2009; Averós *et al* 2010b). This might have resulted in higher mortality, indicating that caution is needed when providing enrichment because, in some instances, there may be undesired consequences. If space allowance increases in housing systems, provision of sufficient objects must be a consideration. Enrichment type is also important, but we could not consider the effects of increased environmental complexity or activity (platforms or tubes) and only included objects, which are assumed to promote gnawing. According to our results (Figure 2[b]) enrichment objects can contribute to controlling the mortality associated with large group sizes.

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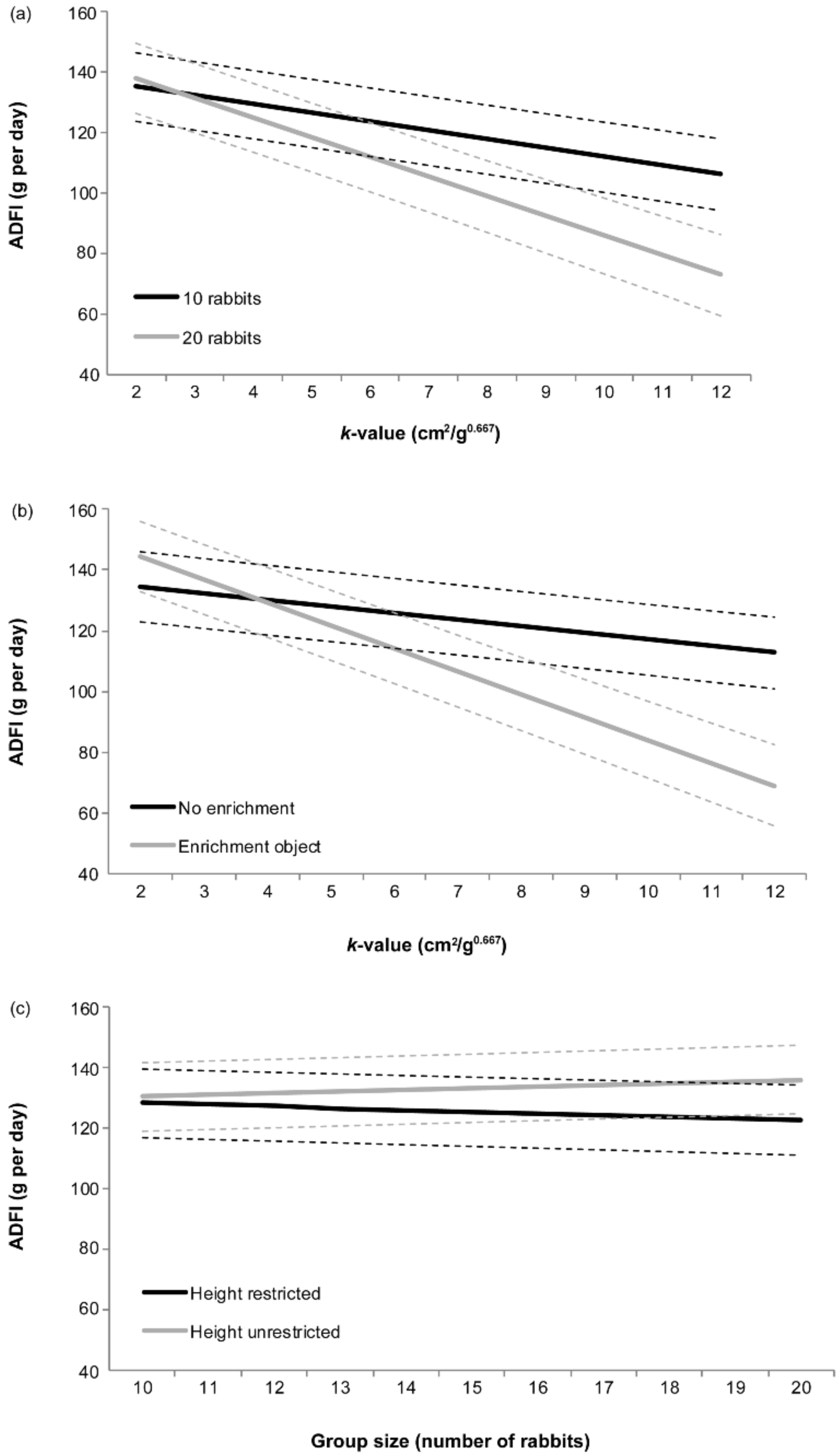
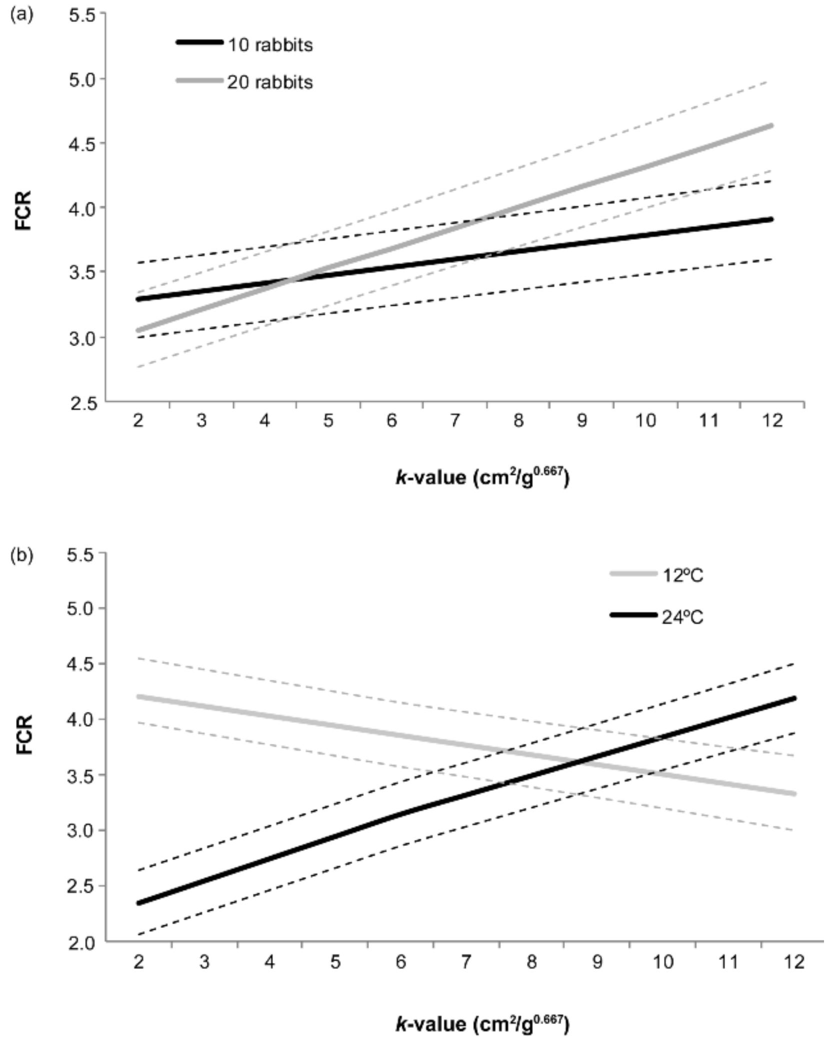
Figure 4



Predicted effect (standard error of prediction in dotted lines) of the interaction between (a) space allowance and group size, (b) space allowance and the use of enrichment object, and (c) group size and height restriction, on the ADFI of growing rabbits (for the median of the other continuous independent variables and covariates). ADFI = average daily feed intake.

Figure 5



Predicted effect (standard error of prediction in dotted lines) of the interaction between (a) space allowance and group size and (b) space allowance and average temperature, on the FCR of growing rabbits (for the median of the other continuous independent variables and covariates). FCR = feed conversion ratio.

A faster decrease in ADFI as space allowance increased was predicted in the presence of enrichment objects (Figure 4[b]), on the grounds that objects might attract the attention that the rabbits would otherwise have paid to the feeder in barren environments. This would have resulted in rabbits eating (and likely spilling) less food, and in a reduction in their growth (Figure 3[b]). The lowest ADFI was also predicted when substrate was provided for feeding purposes, and highest in the absence of substrate, and this influenced growth (Table 6). Fibrous materials have a satiating effect (Frias & Sgarbieri 1998; Cani *et al* 2005), which would account for the reduction in ADFI and ADG when substrate is offered. This appears detrimental from a commercial efficiency perspective, although the economic benefit of reducing feed consumption or spillage might, at least partially, compensate for reduced ADG whilst improving rabbit welfare.

Temperature

We predicted a decrease in ADG and ADFI when temperature increased (Table 6). A reduction in ADFI resulting from heat stress has been described (Chiericato *et al* 1995), as well as increased ADFI at low temperatures (Cervera *et al* 1997) to compensate for a metabolism activation to fight cold. Coefficients (Table 6) indicate that ADG decrease rate is smaller than that of ADFI, so that FCR should decrease as temperature increases. According to Figure 5(b), this should be only expected at a low space allowance. Giving rabbits more space at lower temperatures might promote their movement and easier feeder access, improving their performance.

In summary, we have quantified the manner in which relevant housing aspects affect the behaviour, performance, and mortality of growing rabbits. We think this study is a promising approach to the characterisation of the influence of production systems on the welfare of growing rabbits.

Our conclusions are based mainly on performance and mortality because literature scarcity, and to some extent lack of homogeneity in the way some variables are collected or reported, did not allow inclusion of additional, and perhaps more robust, welfare indicators, such as more specific social behaviours, physiological indicators of stress, or health variables. The effect of allometric space allowance was found to be more important than group size, with increased space allowance promoting higher activity levels and more frequent social interactions. This may be positive for rabbit welfare but may also result in increased aggression. Temperature and appropriate provision of enrichment objects must be considered to avoid undesired effects of more space. Increased space allowance results in poorer performance, particularly in larger groups, which would raise obvious concerns in terms of production, although a reduction in productivity might be, at least partially, compensated through a decrease in feed use and/or wastage. Higher mortalities associated with large group sizes may be compensated through the use of enrichment objects. High temperatures mainly discourage rabbits' movement and reduce performance. The limitations regarding the collection of welfare-specific variables in existing literature are reflected in the present study, and highlight the need for more research to further understand and clarify the effect of housing systems on the welfare of rabbits.

Animal welfare implications

New perspectives for improving the welfare of growing rabbits are offered in this paper. Increased space allowance may be beneficial in terms of welfare, although some considerations must be made. Space allowance needs to adapt to the size of rabbits and change as they grow, and this is why an allometric approach when considering space allowance is proposed. Increased space allowance will only be beneficial if other aspects relative to the housing system are simultaneously considered. A sufficient number of enrichment objects are necessary to keep rabbits occupied and minimise potential aggression due to increased space, and for this the size of the group also needs to be considered. Temperatures within rabbits' comfort zone are also essential. Some system modifications likely to improve rabbits' welfare may be detrimental for the farm productivity, though business schemes exist to encourage improved welfare in commercial settings.

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