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DEVELOPMENT OF HIERARCHY AND RANK EFFECTS IN WEANED GROWING RABBITS (*ORYCTOLAGUS CUNICULUS*)

Vervaecke H.[*], De Bonte L.[*], Maertens L.[†], Tuyttens F.[†], Stevens J.M.G.[‡], Lips D.[*]

[*]KaHoSL. Hospitaalstraat 21. 9100 Sint-Niklaas. Ass. KULeuven. Belgium.
[†]ILVO, Animal Sciences Unit. Scheldeweg 68. 9090 Melle. Belgium.
[‡]Centre for Research and Conservation. K. Astridplein 26. 2018 Antwerp. Belgium.

Abstract: Aggression among growing rabbits reduces production efficiency, and negatively affects the animal's welfare. Understanding hierarchy development may improve its predictive value with regard to differential access to resources and fitness. This could in turn lead to measures to reduce aggression. This study quantifies the development of a hierarchy among small groups of same-age rabbits kept in high density. We describe the development of the hierarchy in four mixed-sex groups formed after weaning at four weeks of age. The relationships between rank and aggressiveness, weight, sex and wound count were examined. To balance possible genetic effects, each group contained four full sibling dyads (N=8) with the male and female coming from the same litter (total N=32). Each group was housed in a wire mesh cage of 0.72 m² and was observed at 4, 6, 8, 10 and 12 wk of age. All activities of focal individuals were scored and antagonistic interactions among all group members were sampled continuously. For rank order analysis, submissive behaviours shown after receiving aggression were used. Females were heavier than males (3.2 kg *vs* 3.0 kg: wk 12); this difference was statistically significant from the sixth week onwards. Two of the four groups developed significantly linear hierarchies from the age of ten and twelve weeks onwards, respectively. In these two groups, rank order did not correlate with body weight, sex or wound count. The group with the steepest hierarchy had the highest number of wounds. The results show that growing rabbits can form linear hierarchies by 10 weeks of age, but this tendency differs strongly among groups. The male and female rabbits did not form separate hierarchies, in contrast to their natural tendencies. This may be due to the high density, and may imply a lack of interaction freedom.

Key Words: rabbit, aggression, dominance, hierarchy.

INTRODUCTION

Aggression among growing rabbits reduces production efficiency, and negatively affects the animal's welfare. Understanding hierarchy development may improve its predictive value with regard to differential access to resources and fitness. This could in turn lead to measures to reduce aggression. The study of dominance hierarchies has received considerable interest in behavioural studies and there is compelling evidence for the relationship between dominance and access to resources, and ultimately between dominance and fitness in carnivores, ungulates and rodents (Dewsbury, 1982; Ellis, 1995). This is true not only of males, but also females (e.g., zebra: Pluhacek *et al*., 2006; Schilder, 1990, baboons: Packer *et al*., 1995; chimpanzees: Pusey *et al*., 1997; rabbits: von Holst *et al*., 2002; and bison: Vervaecke *et al*., 2005).

Correspondence: H. Vervaecke, hilde.vervaecke@kahosl.be
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Correct quantification of a hierarchy may improve the predictive value of this concept with regard to differential resource access and fitness (Drews, 1993; Langbein and Puppe, 2004). It can be expected that the quality of the hierarchy determines the strength of the inter-individual differences in success. Quality of a hierarchy can apply to characteristics of ordinal as well as cardinal dominance rank. Ordinal dominance rank provides information on the linearity of the dominance order, and the consistency of the direction of the interactions among dyads. Cardinal dominance rank quantifies rank distances between individuals, based upon their relative probability of winning or losing dominance interactions (De Vries, 1998). This can be used to calculate a measure of the steepness of the hierarchy (De Vries *et al*., 2006). Dominance relations that are consistent, transitive and stable result in a strongly linear and steep (despotic) hierarchy (as in Van Schaik, 1989). In groups with strongly linear and steep hierarchies, larger inter-individual differences in success in competition for scarce resources are expected (De Vries *et al*., 2006; Vehrencamp, 1983). In the wild, hierarchies tend to be strongly expressed and linear when population densities are high, whereas lower densities relate to weaker hierarchies (Leyhausen, 1971). The study of the quality of dominance relations is complicated by many methodological issues, since the formation and dynamics of dominance relations are influenced by several rank-determining factors, such as sex, age and weight (Drews, 1993). These factors should be taken into account when evaluating hierarchies.

We combined these theoretical insights with the fact that little is known about the development of hierarchy in growing rabbits under commercial mixed-sex conditions.

In this study, we investigated the formation and quality (i.e., both linearity and steepness) of a hierarchy in four mixed-sex groups of growing rabbits formed after weaning at 4 wk of age until 12 wk, the end of the fattening period. The onset of antagonistic behaviour and incidence of injuries was recorded. The relationships between rank and aggressiveness, rank and sex, rank and weight, rank and wound count were examined. The groups were matched to obtain homogeneous groups in terms of sex, age, weaning age, relatedness, and litter.

MATERIAL AND METHODS

Animals

32 New-Zealand rabbits were studied at 4 wk. Four groups were formed, each consisting of 4 males and 4 females. To balance possible genetic effects, each group contained four full sibling dyads (n=8) with the male and female coming from the same litter. Study groups were formed after weaning at 4 wk of age. Ear tags were used for individual recognition. In addition, the ears were colour marked at the beginning of each week. The animals were weighed once per week. Individuals that died prior to the end of the study (one male each from group one, group three and group four, and two females in group three) were omitted from analysis, resulting in 27 subjects at the end of the study (7, 8, 5 and 7 for groups 1, 2, 3 and 4, respectively). The study ended when the rabbits were 13 wk old.

Housing

The animals were kept in groups of eight in a mesh wire cage of 0.72 m² (120×60×30 cm). There were four nipple drinkers and two feeders (25 cm width, 14 cm depth, 27 cm height, content: about 3 kg). Each feeder was divided into three compartments, resulting in simultaneous access by six animals. The animals could consume commercial pellets *ad libitum*. During the first weeks of the study, the animals were administered Bacivet S (Alpharma Belgium) in the water to protect them against enteropathy.

Observation method

The behavioural observations were carried out from mid-September to the end of November 2007. The same groups of eight individuals were observed every 2 wk: at 4, 6, 8, 10 and 12 wk of age. Focal animal observation (10 min) (Altmann, 1974) was carried out with life scoring of all occurrences of all activities of the focal individual (The Observer, Noldus, Wageningen). Simultaneously, continuous sampling of social interactions among all group members, including antagonistic interactions, was performed. Each individual was observed nine times per week, spread over 3 d (Monday, Tuesday and Wednesday). In total, 1324 focals were carried out (total observation duration: 220.67 h). At the start of every observation day, the rabbits were examined for presence and number of wounds.

Ethogram of antagonistic behaviour.

These behaviours were scored continuously for all individuals (Altmann, 1974).

Aggression:

- Bite
- Chase: follow other rabbit
- Initiate circling: displace another individual and continue following it in a circling movement.
- Displace: move in the direction of another individual that yields
- Lunge: brisk movement towards other rabbit
- Snap: biting intention towards another individual

Submission: when the target of aggression pulled away or escaped by fleeing, a submissive interaction was scored. Submission was not scored when the target ignored the aggression without reacting.

Rank order analysis

Hierarchical rank order analysis was carried out with the aid of MatMan, a program for the analysis of sociometric matrices (De Vries *et al*., 1993; De Vries, 1993). For rank order analysis, all possible antagonistic behaviours that were not ignored but followed by a submissive behaviour were used, i.e., eliciting either 'reaction' or 'escape'. There were 79 interactions in group 1, 89 in group 2, 134 in group 3, and 91 interactions in group 4, mostly displacements. The resulting dominance matrix was analysed with MatMan (De Vries *et al*., 1993). In case of significant linearity, the matrix was reordered to find the order most consistent with a linear hierarchy by the I&SI method, which minimises the number of inconsistencies (I) and the strength of inconsistencies (SI) (De Vries, 1998). Dyads that still show a direction of interactions that does not fit the linear order are inconsistent dyads. Circular triads contain an intransitive relationship between any three individuals A, B and C.

Analysis of linearity and directional consistency

The index of linearity h (Appleby, 1983) was calculated and tested against the null hypothesis that linear ranking occurred by chance, by means of a randomisation test in MatMan (De Vries, 1995). Since there were tied or unknown relationships, the improved index of linearity (h') rather than Landau's index was calculated and tested by means of a randomisation test with the aid of MatMan (Appleby, 1983; De Vries, 1995). The directional consistency index (DC) gives the frequency with which the behaviour occurred in its more frequent direction, relative to the total number of times the behaviour occurred (Van Hooff and Wensing, 1987). The total number of times the behaviour occurred in the direction of the higher frequency (H), minus the number of times in the less frequent direction (L), is divided by the total frequency: $DC = (H-L)/(H+L)$. As another descriptive measure, the number of one-way relationships is counted, i.e., the number of dyads in which the behaviour is shown in one direction only, irrespective of the frequency of interaction within the dyads. In two-way relationships, dyadic dominance interactions occurred at least once in both directions (from A to B and from B to A).

Analysis of steepness

David's scores were calculated (David, 1987; Gammell *et al*., 2003), based on the dyadic dominance index (DDI) (De Vries, 1998) as an additional measure of dominance that takes the relative strength of the opponents into account. By normalising these David's scores, they range from 0 to n−1, in which n is the number of animals. These Normalised David's scores, based on the dyadic dominance index (called NDS-DDI values) can then be linearly regressed on the rank numbers of the individuals to calculate the steepness of a hierarchy (De Vries *et al*., 2006). The slope of this linear regression varies from zero to one, in which zero is considered indicative of an egalitarian dominance hierarchy with small rank distances, while a slope of one indicates a strictly despotic dominance hierarchy with large rank differences (sensu Van Schaik, 1989). Steepness was only calculated in case of a linear hierarchy.

Statistical analyses

Kolmogorov-Smirnov tests were applied to evaluate normality or non-normality of the data prior to assigning the appropriate statistical tests, which were performed with SAS-software. *P*-values for significance were set at 0.05. All tests were two-tailed except when indicated differently.

To test whether there was a relationship between weight and sex, analysis of variance (One-way Anova) was performed. To test the relationship between rank and weight, and between rank and wound count, a Spearman rank correlation test was performed. To test the effect of sex on the total number of aggressions performed and received, a Wilcoxon Mann-Whitney-U test was performed. To test the relationship between sex and the occurrence of intra- or intersexual aggressive interactions, Kendall's form of row wise matrix correlations (t_{rw}) and exact right-tailed probability values (p_r) were calculated with MatMan. This row-wise correlation test was performed between the aggression matrix and a hypothesis matrix with the sexes noted as 0 or 1. Statistical analysis: To analyze the relation between rank and age, as well as between rank and weight, a Spearman rank correlation (r_s) coefficient was calculated.

RESULTS

Hierarchy linearity analysis.

The analysis of linearity is based on the submission matrices of the data throughout the weeks (Table 1). Groups 1 and 2 showed a significant linear hierarchy, which was not the case for groups 3 and 4 (Table 2). The low number of unknown relationships shows that in most dyads the antagonistic relationship was clearly expressed. The directional consistency index (value can range between 0 and 1) is not so high in any of the groups, in line with the fairly high percentage of two-way relationships. The significantly linear hierarchies appeared in the two groups from the tenth and twelfth week on.

Steepness analyses

The steepness of the hierarchy was calculated only for the two groups (Groups 1 and 2) that showed a significant linear hierarchy (Figures 1 and 2).

Evolution of aggression in terms of age.

Weekly total number of observed aggressions differed significantly among groups (χ^2=10.127, *P*=0.0161) (Figure 3). Total frequency of weekly observed aggression tended to increase over the weeks from 4 to

Table 1: Submission matrices per group (1, 2, 3 and 4): frequency of submission (see ethogram) by actor (in rows) to receiver (in columns):

	RED 1	RED 2	GREEN 1	GREEN 2	PURPLE 1	PURPLE 2	BLUE 1	BLUE 2
Group 1								
RED 1	0	3	2	0	1	1		1
RED 2	4	0	3	4	1	1		2
GREEN 1	3	4	0	4	4	2		3
GREEN 2	2	3	0	0	1	0		1
PURPLE 1	1	0	2	0	0	2		1
PURPLE 2	3	1	1	2	3	0		3
BLUE 2	3	2	1	1	2	1		0
Group 2								
RED 1	0	1	0	3	2	3	1	1
RED 2	1	0	0	3	1	2	2	1
GREEN 1	2	1	0	5	0	2	2	0
GREEN 2	1	0	0	0	1	0	3	1
PURPLE 1	0	1	0	4	0	3	2	0
PURPLE 2	2	2	1	2	0	0	0	0
BLUE 1	0	2	1	3	2	2	0	0
BLUE 2	5	3	1	4	2	5	3	0
Group 3								
RED 2		0	7	1	1	0	1	2
GREEN 1		14	0	1	0	13	2	8
GREEN 2		2	1	0	0	1	0	1
PURPLE 1		2	2	2	0	0	1	1
PURPLE 2		5	3	0	1	0	2	4
BLUE 1		7	9	0	1	5	0	7
BLUE 2		10	8	0	1	7	1	0
Group 4								
RED 1	0	0	1	0	0	0	4	0
RED 2	2	0	2	2	2	2	3	3
GREEN 1	8	2	0	2	4	0	1	1
GREEN 2	4	1	2	0	0	2	2	1
PURPLE 1	0	5	3	2	0	1	3	0
PURPLE 2	1	0	1	1	0	0	1	1
BLUE 1	3	1	3	1	3	4	0	1
BLUE 2	0	2	0	0	0	3	0	0

Table 2: Linearity analysis.

	Group 1	Group 2	Group 3	Group 4
Linearity index, h’	0.63	0.76	0.59	0.35
unknown relationships, %	11	4	5	11
one-way relationships, %	25	46	28	36
two-way relationships, %	64	50	67	53
Directional consistency index (DC)	0.34	0.55	0.48	0.45
Right tailed probability (*P*-value)	0.05	0.02	0.16	0.48

12 wk, when all groups were considered together (r_s=0.40, *P*=0.0765, n=20). When the groups were considered separately, it was apparent that only group two showed aggression that increased linearly over the five weeks (Group 1: r_s=0.60, *P0*0.2848, n=5; Group 2: r_s=0.90, *P*=0.0374, n=5; Group 3: r_s=0.40, *P*=0.5046, n=5; Group 4: r_s=0,.0, *P*=0.8729, n=5).

Body weight

Except for group 3, there was no correlation between rank and weight of the animals at the end of the observation period (Group 1: r_s=0.07, *P*=0.88, n=7; Group 2: r_s=−0.36, *P*=0.38, n=8; Group 3: r_s=0.90, *P*=0.04, n=5; Group 4: r_s=0,.39, *P*=0.38, n=7; All group: r_s=−0.5, *P*=0.80, n=27).

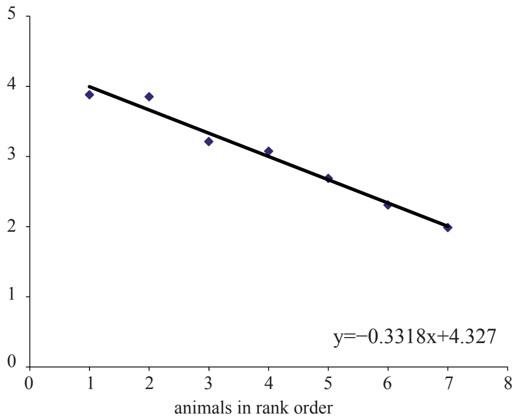

Figure 1: Dominance hierarchy in Group 1 showing the rank distances among the individuals, with ordinal ranks on the X-axis (1=highest rank) and the individual’s normalized David’s scores on the y-axis). The absolute value of the slope of the regression line shows the steepness of the hierarchy (ranging from 0 to 1) (David, 1987; De Vries *et al.,* 2006; Stevens *et al.,* 2007).

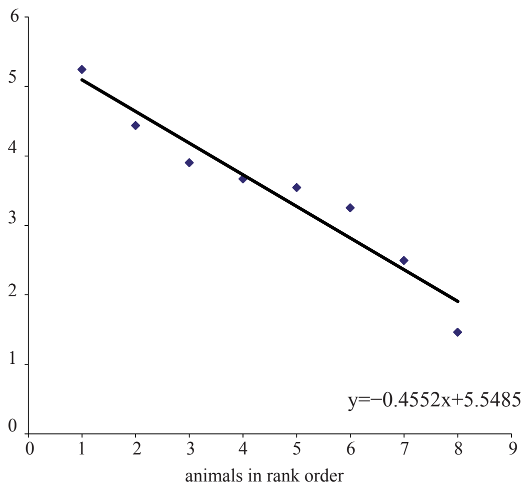

Figure 2: Dominance hierarchy in Group 2 showing the rank distances among the individuals, with ordinal ranks on the X-axis (1=highest rank) and the individual’s normalized David’s scores on the y-axis). The absolute value of the slope of the regression line shows the steepness of the hierarchy (ranging from 0 to 1) (David, 1987; De Vries *et al.,* 2006; Stevens *et al.,* 2007).

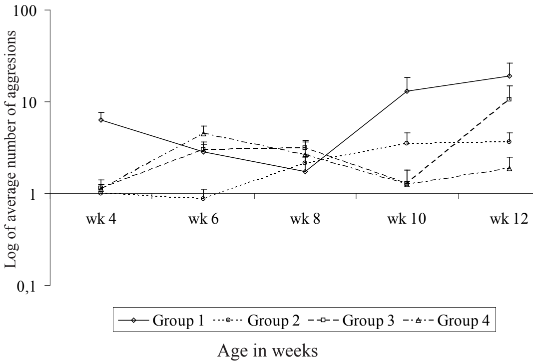

Figure 3: Log of average number of aggressive interactions per group in function of age (expressed in weeks) (± standard error).

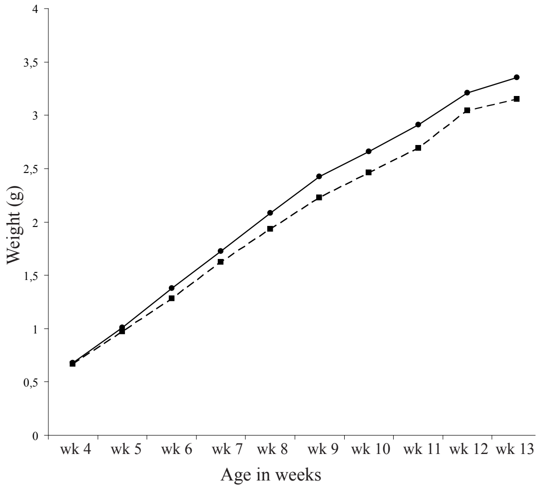

Figure 4: Average weight (expressed in grams) of female (–●–) and male (– ■-) fattening rabbits (mean±standard deviation) in function of age (expressed in weeks).

Females were heavier than males (3.2 *vs* 3.0 kg: wk 12); this difference became significant from the sixth week on (F=4.437; *P*=0.044, df=1). During the entire observation period, the highest weights were noted in the females. In 1 wk, males weighed on average 666 grams, while the females weighed 678 grams. In 13 wk, the males weighed on average 3148 g, while the females weighed 3351 g (Figure 4).

Effect of sex upon rank

There was no difference in total number of aggressions initiated (Z=0.2262; *P*=0.4113) and received (Z=0.755; *P*=0.4702) by males or females. Aggressive interactions were not preferentially directed to same-sex individuals, although there was a trend towards more same-sex interactions in Group 3 (Group 1: t_{rw}=0.14, p_r=0.41; Group 2: t_{rw}=−0.16, p_r=0.25; Group 3: t_{rw}=0.37, p_r=0.06; Group 4: t_{rw}=0.007, p_r=0.48). Neither gender showed significantly different rank positions when the four groups were considered together (Z=−0.1467; *P*=0.9).

Wound count

The first wound was observed in Group 2 when the rabbits were 6 wk old. The average number of wounds per group per week ranged between 0 (i.e., during the first 3 wk) and 2 (7-9 wk). The total wounds over the entire observation period was highest for Group 2 (22 wounds), followed by Group 4 (5 wounds), Group 3 (3 wounds) and Group 1 (2 wounds in total). In Group 4, the first wounds only occurred in 12 wk. Most wounds were bite wounds to the ears. There was no correlation between individual total observed aggression and total wound count (r_s=−0.16, *P*<0.3694, n=32).

The individual weekly number of wounds differed significantly among the four groups (χ^2= 16.6225; *P*=0.0008), with Group 2 differing significantly from the three other groups (post-hoc pairwise tests). There was no difference in total number of wounds received between the sexes (Z=−0.8504; *P*=0.4016). There was no association between ordinal rank and total number of wounds received over the observation period (Rs =0.20, *P*=0.2859, n=30).

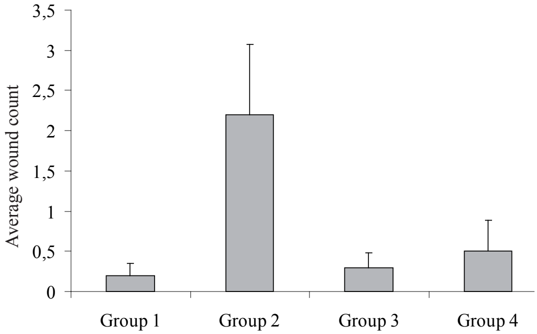

Figure 5: Average wound count per rabbit group (Groups 1, 2, 3 and 4) over the study weeks (mean±standard error).

DISCUSSION

Several studies report separate male and female rabbit hierarchies (Mykytowicz, 1958; Vastrade, 1987). This is seen in free-ranging species where the sexes segregate spatially, except for during the breeding season (e.g., bison: Lott, 2002), or where the priorities regarding competed resources differ (e.g., food versus mates). In rabbits, males compete mostly for access to females, whereas females compete for access to the best nesting sites (Cowan and Bell, 1986, von Holst *et al*., 1999 and 2002). Within male rabbit groups, a linear dominance hierarchy is formed (Garson, 1981; Verberne and Blom, 1981). A male hierarchy develops around 70 d, when the first sexual behaviour is seen, whereas females show little antagonism (Lehman, 1991). A striking finding in our study is that the antagonistic interactions occurred regardless of sex, and that intra-sexual aggression was not more frequent than inter-sexual aggression. Thus there were no separate male and female hierarchies as have been observed in semi-free or in wild rabbits (Mykytowicz, 1958; Mykytowicz *et al*., 1984; von Holst *et al*., 1999; Vastrade, 1987). It is not clear whether the animals in a relatively high density choose to interact equally with both sexes or whether they cannot avoid interactions forced by the high density. It is possible that sex-differentiated social preferences are only expressed after puberty, when priorities differentiate more clearly (e.g., partners for males versus nesting sites or food for females). Semi-naturally housed female rabbits strongly prefer intra-sexual and kin-oriented interactions. It has been suggested that this is a possible mechanism to attenuate the negative consequences of stress (Rödel *et al*., 2006). In the wild, ritualised aggression exhibited at a distance, such as mutual paw scraping and parallel running, can be used to prevent aggressive conflicts. These behaviours are used in territorial inter-male interactions (von Holst *et al*., 1999) and expression of intra-group partner preference for interactions. Held *et al*. (1995) found that low-ranking rabbits do not necessarily prefer a solitary compartment to a group pen. In an experimental setting, rabbits work equally hard to reach social contact as for food (Seaman *et al*., 2008). Although rabbits may prefer group life to single life, the need to maintain differentiated relationships, and the need to avoid interactions by maintaining inter-individual distances, should be examined further. The relationship between aggression, group size and stocking density was studied by Szendrö et al. (2009).

Our results do confirm that rabbits can form linear hierarchies as observed in two of the four groups (e.g., Lehman, 1991). One group (Group 3) nearly reached significant linearity, suggesting that they were developing towards a linear hierarchy, but were doing so at a slower pace than the other groups. The other group (Group 4) that did not reach a linear hierarchy had very few aggressive interactions. This coincided with a period of illness in the group. Verwer *et al*. (2009) found that a stable hierarchy developed from week ten in exclusively male groups (composed of ten animals, housed in large enriched pens). In that study, handled animals formed no linear hierarchy, in contrast with the non-handled animals, which initiated fewer interactions as a group. The variation among groups in linearity of the hierarchy is also apparent in our results, where only half of the groups developed a linear hierarchy.

Between the two linearly organised groups, the most despotic group (Group 2) was also the group with the highest wound count. It was also the group that showed a steady increase in aggression over time. Although the rabbits in Group 1 showed the highest incidence of aggressive behaviour, very few wounds were observed in that group. Overall, aggression did not necessarily increase over time, but in both groups that showed a sudden increase in aggression, it occurred around 10 wk. Aggression in semi-free range rabbits is known to occur from 50 d (Lehman, 1991) and in wild rabbits around 60-90 d (Dudzinski *et al.*, 1977). In rabbit meat production, problems with aggressive behaviour resulting in injury are known to occur at the end of the fattening period between 60 and 90 d, just prior to puberty (Bell and Bray, 1984; Maertens and Van Herck, 2000; Rabillard, 1985) (around 12-14 wk) (Hafez, 1970). Aggression frequency is highest around 80 d (Morisse and Maurice, 1997; Verga *et al.*, 2006; Szendrö *et al.*, 2009), in line with our data, although Heil (1997) reports that biting seldom occurs before 12 wk. For these reasons, it has been suggested that rabbits be slaughtered before the age of 80 d (Rommers and Meyerhoff, 1998). Research showed that the occurrence of injurious aggression can be reduced by offering gnawing sticks (Verga *et al.*, 2004 and 2007; Princz *et al.*, 2009), simple enrichment devices that increase slaughter yield (Dalle Zotte *et al.*, 2009). Our results suggest that these sticks should be provided prior to week ten.

It is unclear which factors influenced the ordinal rank positions of the rabbits in our study. Gender was clearly not a determining factor: neither males nor females systematically dominated the other sex, in contrast to many mammal species (Smuts and Smuts, 1993). In a captive study with rabbits of mixed sexes (one buck and several does), the male seldom engaged in antagonistic interactions with the females and he did not usually win the antagonistic interactions that did occur (Schuh and Hoy, 2004). Weight was also not related to rank, in line with the study by Chu *et al*. (2004) who further found no relation between growth and rank. This study controlled for age, known to be related to a significant dominance determining factor in a study of semi-free range rabbits. The individual rank tended to increase with age throughout the life span (von Holst *et al*., 2002). Lehman (1991) also found that in semi-natural conditions, young rabbits were dominated by older rabbits. All study animals were of similar age. Clearly, a different factor determines dominance among same-aged rabbits. This could be individual personality, quality of mother, or genetic factors. Arteaga *et al*. (2008) suggest further investigation of the possible relation between kits intrauterine position, and later differences in dominance indicators. The advantages related to high rank did not form the scope of our study, but do merit further researcRank related benefits in both sexes in wild rabbits in semi-natural conditions include higher fitness (von Holst *et al*., 2002), increased longevity (von Holst *et al*., 1999), and sexual access: high ranking males interact preferentially with high ranking females (von Holst, 1999), and get sexual access to them (von Holst, 1999). Higher rank in males relates to better immunocompetence and lower adrenocortical activities during periods without group alterations (von Holst, 1999). Conversely, male rabbits with subordinate status showed higher cortisol levels in large groups of male rabbits (Girolami *et al*., 1996). In addition to aforementioned benefits, Arteaga *et al*. (2008) suggest investigation of subtle dominance effects in play, food competition and thermally advantageous positions, which can be relevant welfare-related factors in industrial settings.

Where the hierarchical ranking order may allow for prediction of the order of access to competed resources, it should be investigated whether the dominance style (more or less despotic versus egalitarian) can be indicative of the potential skew in access to resources between high and low ranking individuals among groups.

CONCLUSIONS

Rabbits can form linear hierarchies from the tenth week when kept in small groups at high density. Two groups formed one clear hierarchy independent of the sexes, a pattern that deviates from the natural pattern. There was some difference among groups in speed of development of a hierarchy, in dominance style, in number of aggressions and wounds. Neither sex, weight, nor age were related to rank in these mixed-sex groups.

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