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INHERITANCE OF THE NAKED GENE AND ASSOCIATIONS WITH POSTWEANING PERFORMANCE AND THERMOTOLERANCE CHARACTERS IN FRYER RABBITS FROM AN F_2 GENERATION.

Jackson R., Rogers A.D., Lukefahr S.D.

Dpt. of Animal & Wildlife Sciences, MSC 228. Texas A&M University, Kingsville, TX, USA

Abstract: In 1999, a breeding experiment was initiated with matings of a rare, genetically naked, Mini-Lop buck to New Zealand White does to test the hypothesis that the naked trait was due to a single, autosomal recessive gene. The F_1 generation all had normal fur coats. Parental F_1 X F_1 *inter se* matings were made, which yielded 260 F_2 progeny, 206 furred and 54 naked (79.2 and 20.8%, respectively), supporting the single recessive gene hypothesis (χ^2 = 2.26; df=1; *P*>0.05). Although the F_2 generation was possibly the subject of linkage disequilibrium, another objective was to quantify potential favourable effects of the naked gene on postweaning and thermotolerance characters in fryers over three years (2002-2004) when exposed to hot summers in south Texas (30-35ºC). Weaned fryers (n = 143) from 36 litters were randomly assigned to growing cages containing either two or three furred or naked non-littermates. Models consisted of fixed genetic type (naked and furred classes), year-batch, gender, interactions, and initial age of fryer (linear covariate), and random cage (nested within genetic type), fraternal-litter, and residual variation. Results showed that naked compared to furred fryers had higher ADG (26.7 *vs.* 23.8 g/d; *P*<0.001). However, interaction between genetic type and gender revealed (*P*<0.01) that naked males outweighed furred males (2039 *vs.* 1796; *P*<0.001), whereas females had similar final body weights (1838 *vs.* 1827; *P*=0.8459). For cages of naked compared to furred fryers, feed intake was increased by 25 g/d/fryer (*P*<0.001), but cage feed efficiency (total gain/total feed intake) was poorer (0.232 and 0.266; *P*<0.01), while daily water intake was similar (200 and 192 ml per fryer; *P*>0.05). Furred compared to naked fryers had a higher free water-to-feed intake ratio (2.00 and 1.64 ml/g; *P*<0.001). At 1400 hour, naked fryers had lower rectal temperatures (38.9 and 39.5 ºC) and lower respiratory rates (124 and 162 breaths/minute) compared to furred rabbits, respectively (*P*<0.001). Because of possible effects of linkage disequilibrium, these results are preliminary and need to be confirmed in later generations. Nonetheless, the potential exists to develop a new, niche breed of naked rabbits for arid and tropical environments.

Key words: rabbits, fur, growth, thermoregulation, tropical agriculture.

INTRODUCTION

The rare event of furless or naked rabbits was first reported in Russia by Kislovsky (1928), then from Hammond's population in Britain by Castle (1933), and then much later in France by Boucher *et al.* (1996). Rogers *et al.* (2004) compared performances of rare genetically naked and furred rabbits in the U.S., based on preliminary, first-year data involving F_2 progeny. In general, the furless or naked gene(s) prevents the normal formation of fine wool hairs (underfur), leaving primarily the long and coarse guard hairs (Drapeau, 1933). Rogers *et al.* (2006) reported that naked rabbits produced approximately 90% less fur than normal furred rabbit fryers. In addition, the naked gene appears to differ from the furless mutation (Castle, 1933) in that the rabbit can be entirely devoid of any fur or hair.

Correspondence: S.D. Lukefahr, kfsdl00@tamuk.edu
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Theoretically, furless or naked rabbits could direct more energy towards growth and other metabolic processes rather than to fur production, and have better thermoregulation ability when exposed to periods of extreme heat and humidity. However, the effect of the naked gene has not been previously investigated to determine its potential benefits on rabbit production. Altered trait expressions, such as furless coats, could potentially yield new breeds that are better capable of adapting to hot, arid and (or) humid environments, especially in less developed countries where rabbit development programs exist to benefit limited-resource families.

The research goal of this three-year breeding project was to evaluate the naked gene and its effects on rabbit fryer performance under extreme temperature and humidity stress conditions (subtropical and semi-arid) in south Texas. Specific objectives were: 1) to determine the mode of inheritance of the naked gene; 2) to quantify the effects of the naked gene on postweaning performance traits involving growth, feed and water intake, and survival; and 3) to examine physiological and morphological expressions associated with the naked gene, such as body temperature, respiration rate, and ear length and type. For the second and third objectives, it should be emphasized that the potential existed for linkage disequilibrium involving either naked or furred genes with genes for othercharacteristics; hence, these results are preliminary.

MATERIALS AND METHODS

Population management

The study was initiated in January of 2001 by the donation for breeding of a rare naked Mini-Lop buck born in El Campo, Texas. "Fuzz" (Photo 1), who was mated to commercial New Zealand White (NZW) does, resulting in 16 litters and the birth of 113 F_1 kits. Later, as F_1 parents (13 bucks and 19 does), matings were made *inter se* to produce F_2 progeny to expose the hypothetical single recessive, naked gene. For this purpose, in fall 2001 and spring 2002 through 2004 matings were conducted. Rabbits from large (>10 kits) and small (≤3 kits) litters were crossfostered into fraternal groups. Kits were scored for coat type (normal furred or naked) at 1 wk of age.

Animal management and trait measurements

From the spring of 2002, 2003, and 2004, 143 rabbits (88 furred and 55 naked rabbits) were sampled from 36 litters and were subjected to growth-phase trials, which were conducted during the hottest months of the year (June through August) in order to subject all rabbits to a hot and humid environment to determine possible favorable trait associations with the naked gene. Yearly mean temperatures and relative humidity levels recorded inside the building ranged from 30.2 to 35.1 ºC and 53.7 to 68.9% RH, respectively. Previously at the same location, Medellin and Lukefahr (2001) reported that Altex and NZW kits weaned in summer produced only 15% of fryers weighing at least 1.8 kg by 70 d of age, compared to 88.1, 61.9, and 88.6% in winter, spring, and fall.

All kits were weaned, weighed, and tattooed at a minimum of 28 d of age, and moved as a litter group to a temporary growing cage. When at least three litters had been weaned during the same week (defined as an "age batch" cohort), kits were randomly assigned to experimental cages on the same

Photo 1: The original rare naked rabbit, "Fuzz".

day. In 2002, 2003, and 2004, there were 4, 2, and 1 such age batches as time replications. Each cage was limited to only one kit per fraternal litter. Also, in large litters, a limit of six furred kits were randomly sampled for the study (Table 1). Growing cages (11.8 × 11.8 × 7.1 cm) contained two or three naked or furred fryers. The growth trial was for 42 days for all replications. There were 32 and 20 pens of furred and naked rabbits, respectively.

Rabbits were fed an *ad libitum* supply of a commercial diet (Nutrena Rabbit Pellets, Cargill-Nutrena Feeds Division, Minneapolis, MN) formulated to meet NRC nutrient requirements (NRC, 1977). Cage feed intake was monitored daily, following a 1-wk adjustment period to the growing cages. Water was supplied continuously using 900 ml water bottles to calculate daily water intake per fryer and free water-to-feed intake ratio. During the 42 d growth trial period, outside ambient and inside hutch temperatures were recorded daily at 14:00 h. All rabbits were weighed weekly to monitor growth. At the end of each trial, all naked and furred rabbits had readings taken for ear length and type (0, 1, and 2 for number of erect ears) and for rectal temperature (using a clinical thermometer inserted 6 cm). Respiratory rate was recorded as the number of flank movements per 20 sec, and later was calculated as breaths/min (Thwaites *et al*., 1990). Mortality was recorded throughout the experiment.

Statistical procedures

To test the hypothesis that the naked gene was inherited as a single autosomal recessive, the expected 3:1 phenotypic ratio (furred-to-naked F_2 offspring) was tested by χ^2 using Yate's correction for discontinuity. To analyze individual fryer growth, physiological, and morphological data, the main source was genetic type, consisting of furred and naked classes. The nested, cage within genetic type source served as the error term for testing genetic type for significance ($P<0.05$). Data were blocked for the additional fixed effect of year-batch (seven groups), gender, 1st and 2nd order interactions, and initial age as a linear covariate (mean of 40.7 d, range of 28 to 49 d), corresponding to age when a fryer was formally placed on the study, and the additional random effect of fraternal litter nested within year-batch (added to the model to control variation). For analysis of cage data

Table 1: Distribution of naked and furred weanling rabbits assigned to the experiment.

Year		No. of litters	Naked		Furred		Total
			Females	Males	Females	Males	
2002							
	batch 1	9	5 (2,1,2)[2]	7 (0,3,4)	23	19	54
	batch 2	4	2 (1,0,1)	1 (0,0,1)	9	3	15
	batch 3	3	1 (1,0,0)	3 (0,1,2)	3	5	12
	batch 4	3	2 (0,2,0)	1 (0,1,0)	4	4	11
2003							
	batch 5	3	3 (0,2,1)	2 (0,2,0)	2	2	9
	batch 6	6	5 (1,2,2)	9 (3,4,1)[3]	3	5	22
2004							
	batch 7	8	5 (1,3,1)	9 (2,6,1)	4	2	20
Total		36	23 (6,8,7)	32 (5,17,9)	48	40	143

[1] All naked rabbits were included in the postweaning growth experiment, but a limit of six furred rabbits from the same litter were randomly sampled. [2]Values in parentheses corresponds to the number of Class 1, 2 and 3 naked rabbits (Class 1: little to no fur on the body, head, neck, and feet; Class 2: a light and short coat of fur over the entire body; and Class 3: a light and longer coat of fur over the entire body). [3]One rabbit died in this cohort group before a naked class score could be assigned.

(feed and water variables), the model consisted of only genetic type (naked *vs.* furred classes), year-age batch, and interaction. Data were subjected to REML, mixed-model procedures (Blouin and Saxton, 1990).

RESULTS AND DISCUSSION

Mode of inheritance

F_1 *inter se* matings from fall 2001 and spring 2002 through 2004 produced 260 F_2 progeny (54 naked and 206 furred), which were scored at 1 wk of age, yielding overall observed frequencies of 79.2 and 20.8%, respectively. Our hypothesis was supported (χ^2 = 2.26; df=1; *P*>0.05) that the mode of inheritance for the naked condition is due to a single recessive autosomal gene, which is in agreement with the earlier report by Castle (1933). Interestingly, considerable genetic segregation was observed in the F_2 generation for body size, coat color, ear length and position (e.g., erect or lopped), etc. It should be emphasized that the potential exists for linkage disequilibrium in the F_2 generation involving founder genes linked to either the naked or furred genes, and, if real, it would take several generations to diminish this bias (Falconer and Mackay, 1996). It was further observed that naked rabbits exhibited three distinct versions: Class 1 (21.2%) - little to no fur on the body, head, neck, and feet; Class 2 (48.1%) - a light and short coat of fur over the entire body; and Class 3 (30.8%) - a light and longer coat of fur over the entire body (Photos 2, 3 and 4 respectively). For all three classes, the fur was less dense than that of a normal furred rabbit (Rogers *et al*., 2006). These observations are also consistent with Castle (1933) who reported that the degree of "furlessness" varied among rabbits, presumably due to modifier genes.

From a total of 143 fryers that were subjected to post-weaning growth trials (Table 1), only two weanling fryers died, both of which were naked. Kislovsky (1928) reported that all naked rabbits from one litter in his study died by 1 month of age. However, Castle (1933) observed that the furless gene did not appear to be lethal prior to birth, although furless rabbits were found to be difficult to keep alive and had low fertility. Boucher *et al.* (1996) described seemingly different versions of the furless or naked gene that appeared in three commercial herds in France. However, only one specimen that closely resembled our Class 1 rabbits later died at 80 d of age. The other specimens more closely resembled our Class 3 rabbits, which they described as "hairless". In the same report, autopsies of hairless rabbits revealed several internal maladies, including stomach ulcers, pyloric stricture, and cecal paralysis.

In our population, we surmise that a unique naked mutation possibly exists that does not adversely affect vitality; naked rabbits appeared to be just as healthy as furred rabbits. However, it has been observed that naked kits may be more predisposed to early dermal cysts and eye infections, but ointment treatment applications were successful in preventing permanent injury or blindness. While

Photo 2: Class 1 naked rabbit with little to no fur.

Photo 3: Class 2 naked rabbit with a light coat of fur.

Photo 4: Class 3 naked rabbit with a light coat of fur over entire body.

Table 2: Generalized least squares means for performance traits of naked and furred rabbits.

Trait	Naked	Furred	*P*-value
IW	821±23	782±20	0.1090
FW	1939±37	1811±33	<0.01
ADG	26.7±0.58	23.8±0.52	<0.001
FI	120±3.0	95±2.5	<0.001
FE	0.232±0.008	0.266±0.006	<0.01
WI	200±6.9	192±5.8	0.3560
W:F	1.64±0.05	2.00±0.07	<0.001
BT	38.9±0.03	39.5±0.02	<0.001
RR	124±3.5	162±2.8	<0.001
EL	10.4±0.16	10.5±0.09	0.3506

IW = initial body weight, g; FW = final body weight, g; ADG = average daily gain, g/d; FI = daily feed intake per fryer, g/d; FE = total cagebody weight gains/total cage feed intake; WI = daily water intake per fryer, ml/d; W:F = free water-to-feed intake ratio per fryer; BT = body temperature, ºC; RR = respiratory rate, breaths/min; EL = ear length, cm.

not reported in this paper, subsequent breeding trials have also revealed that naked rabbits are fertile and are capable of rearing young. A relevant factor concerning pregnant naked does is the sparse fur nest component. Although continual fur growth to maturity has been generally observed in naked rabbits from all three classes, additional fur from normal furred does is transferred to complete the fur-straw nest, although artificial materials (*e.g.,* cotton and wool) could be used.

Fryer growth performance

Naked fryers tended (P=0.109) to be heavier initially by 39 g than furred fryers (means of 821 and 782 g; Table 2). Overall, body weights were consistently generally heavier across all six weeks in favor of naked rabbits (Figure 1). Final weights were heavier for naked compared to furred rabbits (1939 and 1811 g; P<0.01). However, significant interactions were detected due to genetic type × year-batch (P<0.05), genetic type × gender (P<0.01) and year-batch × gender (P<0.01). For interactions involving year-batch, no clear pattern was noted upon examination of subclass means. Initially, there was no interaction between genetic type and gender for initial body weight (P>0.05). However, the genetic type x gender effect for final weight revealed that the large difference in final weights between naked

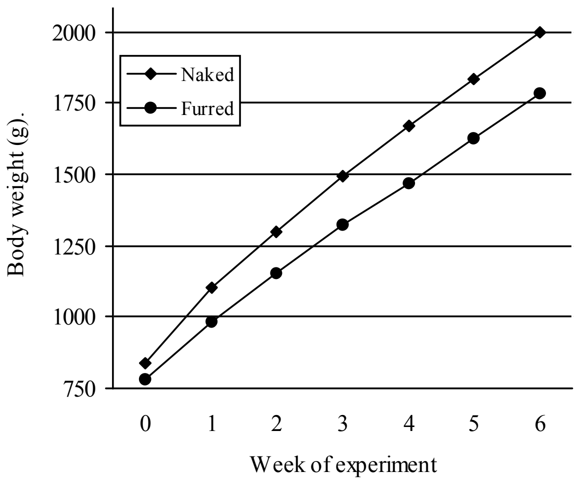

Figure 1: Body weight plots for genetically naked and furred rabbit fryers.

and furred rabbits was gender specific. Figure 2 shows that naked males were heavier than furred males (2039 *vs.* 1796 g; $P<0.001$), whereas naked and furred females had similar final weights (1838 *vs.* 1827 g). Upon closer examination of the least squares means for the largest age batches 1, 6 and 7 (65.7% of the data), naked males were numerically heavier than furred males across these batches, whereas the year-batch × genetic type × gender interaction was not significant.

Further research is now under way to elucidate the genetic and physiological mechanisms manifested between the naked gene and testosterone. A plausible hypothesis is that the degree of fur loss, as well as growth, may be to some extent associated with testosterone production in naked male rabbits. If this same hypothesis can be applied to Class 1, 2, and 3 male rabbits, a supplemental analysis was performed (although data are sparse). Class 1, 2, and 3 naked males had mean final body weights of 1724±101, 2120±59, and 1945±72, compared to furred males of 1772±46 g. To explain why Class 1 naked males had similar body weights to furred males, an observation was made that Class 1 naked rabbits appeared to have reduced feeding behaviour. Perhaps even less fur on the foot pads affected their mobility on the cage wire floors. A useful study would involve the rearing of naked and furred rabbits on non-wire cage floors to re-examine body weight and feed intake performance.

In general, naked rabbits had higher rapid ADG than their furred counterparts, 26.7 and 23.8 g/d ($P<0.001$). The only significant interaction for ADG was gender × year-batch ($P<0.01$). Unlike final body weight, the genetic type × gender interaction effect was not detected for ADG, perhaps due in part because naked male rabbits tended to be heavier initially than furred rabbits (850 *vs.* 788 g, difference of 62±31 g; $P=0.0501$). In a previous experiment also conducted during the summer months, Ruiz-Feria and Lukefahr (1998) reported on the effect of electrical fur clipping of fryer rabbits, which significantly increased ADG by 1.7 g/d and final body weights (approximately 70 d of age) by 73 g compared to furred (non-clipped) controls. The authors associated the fur clipping effect with higher feed intake (difference of 112 g/d), presumably due greater temperature/humidity suppression (lower critical temperature zone).

Feed and water utilization

Daily feed intake per fryer was greater in cages of naked than in cages of furred rabbits (least squares means of 120 and 95 g/d, respectively; $P<0.001$). This result reinforced our hypothesis that naked rabbits would consume more feed due to less heat-humidity stress (*i.e.,* higher critical temperature zone). However, the greater feed intake may have contributed to a higher heat increment as associated with the high fiber diet (38.2 and 20.3% NDF and ADF) because naked rabbits had poorer feed conversion rates (0.232 and 0.266; $P<0.01$).

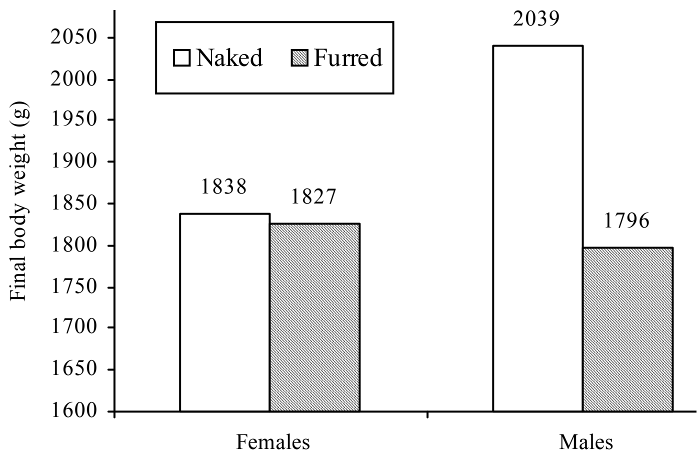

Figure 2: Final body weight means by genetic type (naked and furred) and gender.

Paradoxically, water intake per fryer in cages of naked compared to furred rabbits was not statistically different (200 and 192 ml/d). In reference to the general positive association between feed and water intake, Eberhart (1980) cited in Lebas *et al*. (1997) reported that from 18 to 30ºC, fryers consumed less feed (158 and 123 g/d) and had slower growth (37.4 and 25.4 g/d), while water intake rose from 271 to 386 g/d, respectively. Cages of naked compared to cages of furred fryers had a lower free water-to-feed intake ratio of 1.64 and 2.00 ml/g (P<0.001). Similar to the value of 2.00 for furred fryers, Jin *et al.* (1990) reported a free water-to-feed intake ratio of 2.30 for NZW fryers reared in an environmentally controlled room at 30ºC.

It is plausible that furred fryers needed less free water to digest the lower quantity of ingested feed, but required more water to dissipate their higher body temperature. To support this explanation, in the first and largest year-batch cohort involving 18 out of 52 total cages, simple correlation coefficients between feed and water intake (calculated on a per fryer basis) were 0.68 and 0.02 for cages of naked and furred rabbits, respectively. While the 0.68 correlation is certainly reasonable, the unreasonable 0.02 correlation from furred rabbits may possibly reflect an impaired state of thermal homeostasis. In future trials, it would be useful to monitor water intake hourly rather than on a daily basis.

Conversely, in a colder climate, Boucher *et al.* (1996) also reported that hairless or naked rabbits appeared to have poor feed conversion due to excessive energy or radiation loss associated with thermoregulation, since fur is known to help insulate body temperature. However, this is not an issue in arid and tropical environments where it seldom freezes. Indicative of diverse comfort or thermoneutral zones, at 1400 hr, the behavior of naked rabbits appeared normal (mobile and alert), whereas furred rabbits were typically in a laying, stretched position, panting to dissipate body heat.

Physiological response

Naked rabbits had lower core body temperatures at 1400 hr than furred rabbits (means of 38.9 and 39.5ºC; P<0.001). Across all but one replication, naked rabbits had a clear advantage over furred rabbits by displaying lower body temperatures. The exception was on the last day of replication seven when the ambient temperature was 38 ºC (Figure 3); both naked and furred rabbits had similar mean body temperatures, although respiration rate was considerably lower for naked rabbits (Figure 4).

Boucher et al. (1996) reported that naked rabbits had lower body temperatures than furred rabbits (37 and 39 ºC), although ambient temperature or time of year information was not provided. In the

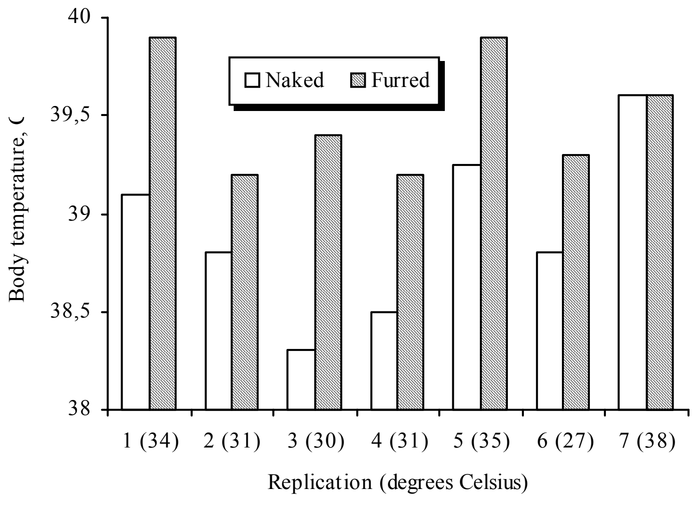

Figure 3: Body temperature of naked and furred rabbits on the last day of each 6-week experimental replication at approx. 1400 hour.

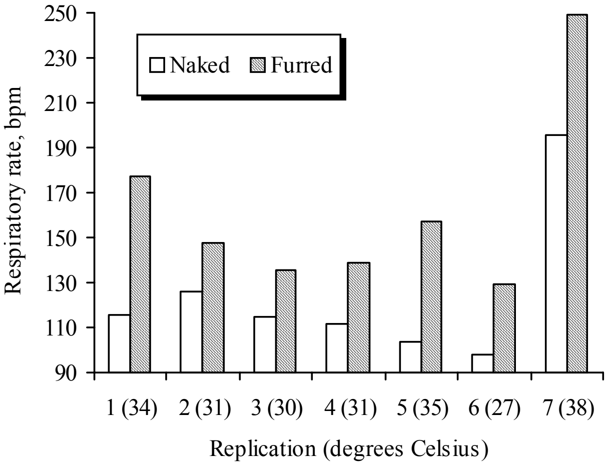

Figure 4: Respiratory rate (breaths/minute) of naked and furred rabbits on the last day of each 6-week experimental replication at approx.

present study, respiratory rates were lower in naked than in furred rabbits (124±3.5 and 162±2.8 bpm; $P<0.001$). Finzi *et al.* (1992) reported that sheared compared to non-sheared NZW bucks took 180 and 220 bpm when placed for 5 h in climatic chambers at 30 ºC and 75% RH. In the present investigation, the more normal temperatures and respiratory rates exhibited by naked rabbits indicated a functional thermoregulation system (*i.e.,* higher critical temperature zone), whereas furred rabbits clearly had impaired thermal homeostasis.

Associations of ear length and type

In a separate analysis involving year-batch 1 data, which was the largest data subset (n = 92 rabbits), initial ear length (for both ADG and final body weight) and initial body weight (for ADG only) were added to the model as linear covariates to determine associations with postweaning growth traits. Results revealed ($P<0.001$) that overall for every 1 cm increase in initial ear length, ADG and final body weight increased by 2.2 g/d and 199 g, respectively. However, the slopes of the individual class regression lines were parallel ($P>0.05$) for both covariates between naked and furred rabbits. Lukefahr and Ruiz-Feria (2003) reported distinct associations between ear length and ADG in fur clipped compared to non-clipped fryer rabbits (2.72 *vs.* 1.33 g/d for every 1 cm increase in ear length). In the same report, fur clipped rabbits that had a minimum ear length of approximately 10 cm showed a declining trend in core body temperature. In contrast, Finzi *et al.* (1986) found no relationship between ear width and body temperature in NZW rabbits subjected to 30 ºC in climatic chambers for 100 min; however, there was no mention of air circulation in the chambers, which is critical for proper ear function in thermoregulation. Also, not adjusted for initial body weight, means for final ear length were similar ($P>0.05$) between naked and furred rabbits (10.4 and 10.5 cm). However, at a constant initial body weight, initial ear length differed ($P<0.001$) between naked and furred rabbits (7.41 and 7.81 cm, respectively).

In a supplemental analysis, ear type class (0, 1 or 2 = none, one or two ears erect) was scored at the end of each 6-wk growth trial, and added as a fixed effect in growth trait models. The rationale for this analysis was based on the hypothesis that rabbits with erect ears should be better able to lower their body temperature than rabbits with non-erect ears under a typical, prevailing afternoon breeze situation. Results revealed that rabbits with lopped-ears (both ears non-erect) had more rapid body gains ($P<0.05$) and tended ($P=0.0781$) to have heavier final weights (least-squares means of 1,965 g [n = 17 rabbits]) than rabbits with one (1,844 g [n = 49 rabbits]) or both ears erect (1,906 g [n = 25 rabbits]). No interaction was detected ($P>0.05$) between genetic type (naked and furred) and ear type class. However, in commercial herds, the fastest growing fryers typically have lopped ears, albeit temporarily, so it is not possible to surmise whether this finding is attributable to better heat tolerance or thermoregulation *per se*, to linkage disequilibrium, or is simply a characteristic of faster growing rabbits.

CONCLUSIONS

These preliminary results tend to favor genetically naked rabbits. However, these experimental results need to be confirmed in later generations to ensure minimum bias due to possible linkage disequilibrium. However, present results do not appear to support the view that certain founder genes for growth or ear type were closely linked to either the naked or furred genes. The original naked, Mini-Lop buck had a mature weight of only 2.99 kg, and of course he had lopped ears. Grobner *et al.* (1985) reported that Mini-Lop does, as expected, had substantially lighter mature body weights than NZW does (3.39 and 4.89 kg, respectively). In the present study, naked fryers had generally higher ADG than furred fryers, and fryers with lopped ears tended to be heavier than fryers with either one or 2 lopped ears. Moreover, since naked fryers had approximately 90% less fur than furred fryers (Rogers *et al.* (2006)), naked fryers would be expected to have lower body temperatures and respiratory rates when exposed to heat-humidity stress conditions, that indirectly could enhance feed intake and growth performance. Further studies will continue to (re)examine our rare naked rabbits for these and other vital characteristics of adaptation. The potential exists to develop a new, niche breed of naked rabbits for arid and tropical environments.

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