Glucose metabolism and adrenal function in goats bred for fibre production (Angora goat) or meat production (Boer goat)

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It has been proposed that the abortions, cold-stress fatalities, and slow growth rates typical of the South African type of Angora goat can be explained by congenital adrenal hypofunction incident to genetic selection for hair production. The aim of this experiment was to compare glucose metabolism and adrenal function in Angora goats vs. Boer goats under a range of dietary conditions. Glucose plasma concentration was 7% lower in Angoras ($P < 0.01$). Glucose flux rate was increased by dietary level ($P < 0.01$), and there was an interaction between breed and diet ($P < 0.05$). The rate of increase in glucose flux rate with increasing dietary energy level was slower in Angoras. The amount of glucose in the metabolic pool was 8% more in Angoras ($P < 0.05$), and this was distributed throughout a 17% larger volume of body fluid ($P < 0.01$). Both pool size and volume of distribution increased ($P < 0.05$) with level of feed. Glucose clearance rate did not differ between breeds ($P > 0.05$), and there was no evidence of impaired adrenal function in Angora goats following glucose loading. Acetate clearance rate was 20% slower ($P < 0.01$) in Angora goats. There was a positive linear ($P < 0.05$) relationship between acetate clearance rate and diet, but no interaction ($P > 0.05$) between breed and diet. Although much of the data reported is consistent with impaired gluconeogenic capability, no evidence of adrenal hypofunction could be found. It was concluded that a more likely hypothesis would be that selection for hair production has resulted in a shift in the partitioning of amino acids away from gluconeogenesis towards hair-protein synthesis to the extent that the Angora goat may be unable to mobilize sufficient endogenous protein reserves rapidly enough for gluconeogenesis during times of sudden demand.

Daar is voorgestel dat die aborsies, kouestresvrektes en stadige groeitempo's wat kenmerkend van die Suid-Afrikaanse-tipe Angorabok is, aan 'n toestand van adrenaal-ontoereikendheid toegeskryf kan word as gevolg van volgehoue genetiese seleksie vir haargroei. Die doel van hierdie proef was om die glukosemetabolisme en adrenaalfunksie van die Angorabok met dié van die Boerbok onder 'n reeks voedingstoestande te vergelyk. Glukoseplasmakonsentrasie was 7% laer in die Angorabok ($P < 0.01$). Glukose-omsettempo is deur dieetvlak ($P < 0.01$) versnel, en daar was 'n interaksie tussen ras en dieet ($P < 0.05$). Die mate waartoe glukose-omsettempo deur dieet verhoog is, was laer in die geval van die Angorabok. Die hoeveelheid glukose teenwoordig in die metaboliese poel was 8% meer in die Angora ($P < 0.05$), en dit was deur 'n 17% groter volume van vloeistof versprei ($P < 0.01$). Beide poelgrootte en verspreidingsvolume van glukose is deur toenemende dieetvlak verhoog ($P < 0.05$). Glukoseverwyderingstempo het nie tussen rasse verskil nie ($P > 0.05$), en daar was geen tekens van verswakte adrenaalfunksie ná glukose-lading in Angorabokke nie. Asetaatverwyderingstempo was egter 20% stadiger in die Angorabok ($P < 0.01$). Daar was 'n positiewe lineêre verwantskap ($P < 0.05$) tussen asetaatverwyderingstempo en dieet, maar geen interaksie tussen ras en dieet nie ($P > 0.05$). Alhoewel baie van die data wel met verswakte glukoneogeniese vermoë samehangend is, kon geen getuienis van adrenaal-ontoereikendheid gevind word nie. 'n Meer waarskynlike hipotese is dat seleksie vir haarproduksie tot 'n verskuiwing in die verdeling van aminosure weg van glukoneogenese na haarproteïensintese gelei het, tot so 'n mate dat die Angorabok nie die vermoë besit om proteïenreserwes vinnig te mobiliseer tydens periodes van verhoogde behoefte soos kouestres en dragtigheid nie.

Keywords: Acetate, adrenal, glucose, goat, metabolism, nutrition, ruminant, selection.

Introduction

In a discussion about the need for future research on goats, Charlet (1981) stressed the need for information on the physiological basis of nutrition and the genetic determinants of factors such as level of hormone secretion. In the case of the Angora goat, tables of nutritional requirements (NRC, 1981) have been derived by extrapolation from data obtained from other breeds of goat, and there is little reliable information available for the formulation of breeding aims (Erasmus, 1987). The need for research on these aspects is emphasized by the results of Herselman (1990), who found that energy requirements for hair production appear to be three times higher than previously estimated, and suggested that this was due to adrenal hypofunction consequent to genetic selection for increased hair production. The fact that adrenal corticosteroids are known to decrease hair growth rate and fibre diameter may explain the association which has been observed between reduced adrenal function and increased mohair production (Van Rensburg, 1971). Adrenal hypofunction is also consistent with the high incidence of abortions (Van Rensburg, 1971; Wentzel *et al.*, 1976; Wentzel, 1986) and cold-stress related fatalities (Wentzel *et al.*, 1979) prevalent among South African Angora goats. The consistently lower urea excretion rate of the goats used in this experiment (Cronjé, 1992) is suggestive of an impaired rate of gluconeogenesis from amino acids, which is also typical of adrenal hypofunction. However, direct evidence for the adrenal insufficiency hypothesis is tenuous. The present experiment was conducted to investigate this hypothesis by comparing the adrenal function and glucose metabolism of the Angora goat to that of a breed which has been selected exclusively for meat production (Boer goat).

Experimental Procedures

Five Angora goat ewes (mean live mass 24 kg, *SE* = 1), and five Boer goat ewes (mean live mass 57 kg, *SE* = 2.8), 12—18 months of age, were fed each of five levels of a diet in a cross-over design with five periods. The pelleted diet was formulated to contain 12 g CP/MJ ME (9.9 MJ ME/kg; 119 g CP/kg) and was fed to provide 77, 88.5, 100, 111.5, or 123% of maintenance energy requirements (0.424 MJ/kg $W^{0.75}$/d; NRC, 1981). For further details, see Cronjé (1992). Animals were housed indoors in metabolism crates and fed at two-hourly intervals with automated feeders. Animals were allowed to adapt to new diets for a period of 10 days before commencement of measurement periods which lasted for five days.

Faeces collections were begun on the first day of the measurement period and continued for the following four days. Faeces were collected daily, weighed and 10% subsamples were added to a bulk sample which was then frozen. Organic matter (OM) content of faeces and feed was determined using standard (AOAC, 1984) methods.

Catheters (1 mm ID / 2 mm OD; Dural Plastics, Australia) were inserted into each jugular vein on the second day. On the third day, a single intravenous injection of D-[2-^{3}H]-glucose was administered for estimation of glucose kinetics. The dose contained 180 μCi D-[2-^{3}H]-glucose and 0.45 mg carrier glucose in 5 ml sterile saline solution (9 g NaCl/l). Blood samples were taken from the contralateral catheter before the injection and at 1, 1.5, 2 and 2.5 h thereafter. Heparinized samples were centrifuged at 1000.G, and the plasma was removed and frozen until analysis. For radioactivity counting, samples were deproteinized by the Somogyi–Nelson procedure, and glucose was isolated as the penta-acetate derivative (Jones, 1965). Filtrates were counted in 10 ml scintillation fluid which consisted of 4 g PPO (2.5-diphenyloxazole), 0.2 g POPOP (1.4-bis-[2(5-phenyloxazolyl)]-benzene) in 1 000 ml toluene. All samples were quench-corrected for counting efficiency using the external standard method. Glucose plasma concentrations were determined using the glucose oxidase method (Boehringer Mannheim). Glucose kinetics were calculated according to procedures described by Nolan & Leng (1974).

On the fourth day, a single intravenous injection of [^{14}C]-urea was administered for determination of urea kinetics, the results of which are presented elsewhere (Cronjé, 1992).

Acetate clearance rates were determined on the fifth day of the experimental period. An aqueous solution of glacial acetic acid designed to supply 4 mM acetate/kg live mass was adjusted to pH 7 with NaOH, made up to 50 ml with distilled water and injected intravenously over three minutes. Blood samples were collected into heparinized tubes on ice before the injection and at 10-min intervals for 60 min thereafter. Plasma was separated by centrifugation at 1000.G, and deproteinized using sulphosalicylic acid (0.1 ml 50% *w/v* solution per ml plasma). The deproteinized plasma was decanted and 250 μl 3N NaOH was added per 2-ml sample in order to raise the pH to 10. Samples were stored frozen until analysis by gas chromatography. Clearance rate was calculated as the slope of the semi-log regression of ln acetate concentration (mM) vs. time (min).

On completion of the experiment, all animals were fed the same diet as used previously, but at the estimated maintenance energy level. Glucose clearance rate was then determined. The glucose load (0.4 g/kg live mass) was injected intravenously over 1 min as a 50% (*w/v*) solution in saline. Blood samples were collected prior to the injection and at 15, 30, 60, 120, 180, 240, 300, 360 and 420 min thereafter. Glucose plasma concentrations were determined as described above. Clearance rate was calculated as the slope of the semi-log regression of ln glucose increment (concentration minus pre-injection concentration) vs. time (min).

Statistical analysis

Results were analysed as for a cross-over design and were tested for polynomial effects, using a mixed model least-squares and maximum likelihood computer program (Harvey, 1988).

Results

Treatment means and statistical significance of main effects are shown in Table 1. Mean organic matter digestion was 4% lower in Angoras ($P < 0.01$) than in Boer goats. Plasma glucose concentration was 7% lower in Angoras ($P < 0.01$), and was not affected by diet. When expressed on a metabolic weight basis, glucose flux rate was increased by dietary level ($P < 0.01$), and there was a significant ($P < 0.05$) linear × linear interaction between breed and diet. Figure 1 shows that the rate of increase in glucose flux rate (g/d) with increasing dietary energy level was slower in Angoras than in Boer goats. The regression equations are:

Angora goat: $Y = 20.06 + 0.4696.D$
$(se) \quad (6.93) \quad (0.0684)$
$R^2 = 92.0\%; P < 0.005$

Boer goat: $Y = -12.1 + 1.350.D$
$(se) \quad (16.2) \quad (0.160)$
$R^2 = 94.6\%; P < 0.005$

The mean amount of glucose in the metabolic pool (g/kg $W^{0.75}$) was 8% larger in Angoras ($P < 0.05$), and this was distributed throughout a 17% larger volume (l/kg $W^{0.75}$) of body fluid ($P < 0.01$). Both pool size and volume of distribution (/kg $W^{0.75}$) were increased ($P < 0.05$) by increased level of feed.

Glucose clearance rate for Angora goats (1.999%/min, *SEM* 0.13) did not differ significantly ($P > 0.05$) from that for Boer goats (2.423%/min, *SEM* 0.26). Glucose plasma concentrations were elevated three- to four-fold within 20 min following injection of the glucose load (Figure 2). Concentrations typically fell below pre-injection levels within 3 h, following which concentrations rose again to reach baseline levels within 5—6 h. Although there were large differences in response to glucose loading between individuals, there was no apparent difference between breeds in the ability to restore glucose concentration to a level at or near baseline following the initial decrease to levels below pre-injection concentrations (Figure 2).

The mean pre-injection acetate plasma concentration was 1.04 mM (*SE* 0.07), and there were no differences between breeds or diets ($P > 0.05$). Acetate clearance rate was 20%

Table 1 Effects of feed intake level on organic matter digestibility, glucose kinetics and acetate clearance rate in Angora vs. Boer goats

		Dietary energy level (% of maintenance energy)							Significance of effect[1]		
	Breed	77.0	88.5	100.0	111.5	123.0	Mean	SEM[2]	Breed	Diet	Inter-action
OM digestion (%)	Angora	76.00	78.40	77.20	78.00	80.60	78.04	0.4502	**	*	NS
	Boer	80.20	80.80	81.80	81.00	80.80	80.92	0.4502			
Glucose concentration (mg/ml)	Angora	0.594	0.570	0.606	0.606	0.592	0.5936	0.008629	**	NS	NS
	Boer	0.626	0.644	0.640	0.662	0.624	0.6392	0.008629			
Glucose flux rate (g/d)	Angora	58.41	58.61	66.21	74.40	77.54	67.04	1.863	**	**	**
	Boer	96.68	104.8	119.4	133.6	159.9	122.85	1.863			
Glucose flux rate ($g/d/kg\ W^{0.75}$)	Angora	5.319	5.338	6.030	6.792	7.175	6.131	0.1142	NS	**	*
	Boer	4.643	5.121	5.798	6.572	7.749	5.977	0.1142			
Glucose pool size (g)	Angora	3.660	3.806	3.640	3.852	4.062	3.804	0.1008	**	**	NS
	Boer	6.164	6.474	6.506	6.806	7.056	6.601	0.1008			
Glucose pool size ($g/kg\ W^{0.75}$)	Angora	0.3334	0.3443	0.3312	0.3506	0.3751	0.3469	0.007097	*	*	NS
	Boer	0.2972	0.3166	0.3160	0.3341	0.3408	0.3209	0.007097			
Glucose volume of distribution (l)	Angora	6.182	6.714	6.066	6.364	6.830	6.431	0.1523	**	*	NS
	Boer	9.810	10.012	10.118	10.442	11.236	10.324	0.1523			
Glucose volume of distribution ($l/kg\ W^{0.75}$)	Angora	0.5615	0.6070	0.5513	0.5780	0.6304	0.5857	0.01085	**	*	NS
	Boer	0.4732	0.4887	0.4904	0.5144	0.5431	0.5020	0.01085			
Acetate clearance rate (%/min)	Angora	4.204	4.065	4.533	4.959	4.510	4.454[a]	0.1755	**	*	NS
	Boer	5.003	5.204	5.927	5.162	6.520	5.563	0.1686			

[1] ** $P < 0.01$; * $P < 0.05$; NS = not significant ($P > 0.05$).

[2] SEM = Standard error of the mean; n = 25.

[a] n = 24.

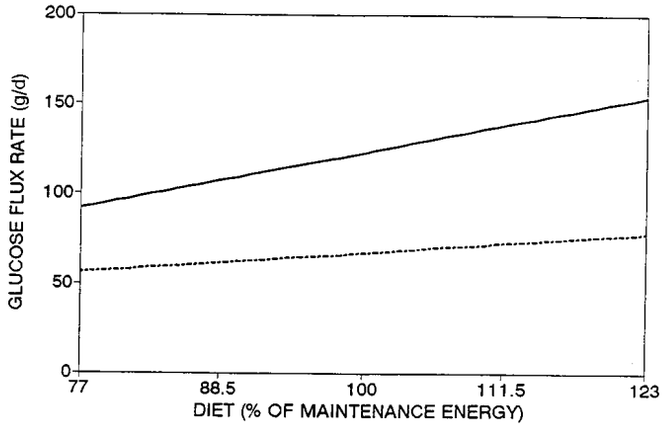

Figure 1 Regression of glucose flux rate on level of diet for Angora goats (------) and Boer goats (——). For details see text.

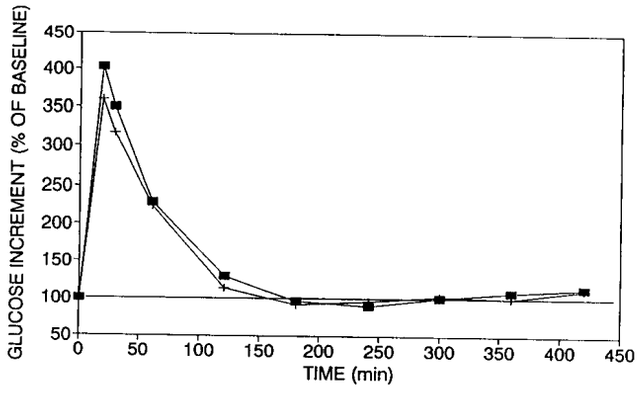

Figure 2 Time-course of mean glucose plasma concentrations following intravenous administration of a glucose load in Angora goats (+) and in Boer goats (■). (Glucose concentrations are expressed as a percentage of pre-loading concentrations.)

slower ($P < 0.01$) in Angora goats (mean: 4.46%/min, *SE*: 0.18) than in Boer goats (mean: 5.56%/min, *SE*: 0.16). Regression analysis showed a positive linear ($P < 0.05$) relationship between acetate clearance rate and diet; there was no interaction ($P > 0.05$) between breed and diet.

Discussion

Van Rensburg (1971) proposed that progress in genetic selection for hair growth rate in the Angora goat has, in reality, been made as a result of indirect selection for lowered adrenal function. An inability to sustain adequate blood glucose concentrations appears to be a common factor linking cold-stress mortalities (Wentzel *et al.* 1979) and nutritionally induced abortions (Wentzel *et al.*, 1976) in the Angora goat. These results are consistent with the aetiology of adrenal hypofunction (for aetiology, see Frawley, 1967; Rijnberk & Mol, 1989), as is the lower glucose plasma concentration in Angora goats which was observed in this study. However, the lower glucose concentration could also simply be due to

dilution of an equivalent amount of glucose throughout a larger volume of fluid, as the volume of glucose distribution was larger in Angoras. In fact, the amount of glucose present in the sampled compartment (pool size) was higher in Angoras. Although the volume of distribution for glucose is assumed to be equivalent to extracellular fluid volume (Bergman, 1963), there is evidence that glucose is distributed throughout at least two other compartments which are connected with this compartment (Leng, 1970). Thus, although the values given here are related to the extracellular fluid compartment, they may also be functions of the size and turnover rates of other compartments which are biologically undefined (White *et al.*, 1969). None the less, it is significant that a larger glucose volume of distribution is, in itself, consistent with a deficiency of adrenal glucocorticoids relative to insulin secretion, as glucose volume of distribution is known to be increased by 50% or more by insulin injections (Bergman, 1983). Caution should, however, be exercised in relating lower blood concentrations of glucose and other metabolites such as cortisol to adrenal function without further qualification. Measurement of the actual production rate of glucose (glucose flux rate) and responses to adrenal challenges such as the glucose tolerance test would provide a more fitting measure of adrenal sufficiency.

Glucose flux rate was increased in both breeds by increasing feed intake. This is consistent with other reports which show that glucose flux rate in ruminants increases in proportion to dietary energy intake (Leng, 1983) and protein intake (Cronjé *et al.*, 1992). The rate of increase in glucose flux rate with increasing level of diet was slower in Angoras than in Boer goats. This could be due to several factors: Although the 4% lower OM and 5% lower N (see Cronjé, 1992) digestion observed in the Angora may have contributed to the slower increase in flux rate, it is unlikely that this would have had a major effect, as the amount of glucose supplied by the portal drained viscera is thought to contribute only 1% of body glucose production under most circumstances (Bergman, 1983). The bulk of glucose produced in the ruminant is derived by gluconeogenesis from the liver (87%) and kidneys (9%). Over 90% of the propionate absorbed is removed by the liver, and this source may be responsible for 30—60% of glucose production (Bergman, 1983). Amino acids may be responsible for 15—32% of glucose production from the liver, and 2—4% of glucose produced in the kidneys; glycerol may account for 5% of glucose produced, and lactate for 15% (Bergman, 1983). Unless the lower OM digestion observed was associated with a considerable shift in rumen microbial metabolism towards a lower propionate production rate, a reduced rate of gluconeogenesis from endogenous amino acids would appear to provide the most likely explanation for the slower rate of increase in glucose flux rate in Angoras. Although speculative, this explanation is consistent with the lower urea excretion and higher nitrogen retention reported previously (Cronjé, 1992) for the Angora goat.

While much of the data presented here could be construed as symptomatic of a low secretion of glucocorticoids, none of these measurements can be regarded as diagnostic for adrenal hypofunction. A glucose tolerance test was carried out to detect any abnormality in glucocorticoid or insulin metabolism. In humans, the response to a glucose tolerance test in patients with adrenal insufficiency or islet cell tumours (oversecretion of insulin) appears normal over the first three hours, but glucose concentrations continue to fall during the fourth and fifth hours (hypoglycaemic tail) (Caraway, 1982). In this study there were no differences in the rate of clearance of the glucose load, nor was there any suggestion of a hypoglycaemic tail with either breed.

The fractional clearance rate following glucose loading (1.999%/min) was slightly higher than that recorded in this study using ^{3}H-glucose without loading (1.22/min), but similar to that reported for cattle (1.98%/min; Kaneko, 1989). By way of contrast, glucose clearance rate dropped from 1.27 to 0,44%/min in fasted ewes (Van der Walt *et al.*, 1980) and may fall as low as 0.38%/min in diabetic cows (Kaneko, 1989). The diagnostic significance of these results may also be judged by the fact that the glucose tolerance test is not performed in humans unless the patient has received a glucocorticoid hormone prior to the test because the degree of reactive hypoglycaemia in patients with adrenal corticoid insufficiency may precipitate severe fibrile reaction (Frawley, 1967). It would thus appear that adrenal function and insulin secretion were normal in the animals examined.

The reported inability of Angora goats to sustain blood glucose concentrations at normal levels following sudden exposure to cold or deprivation of food could also be due to an inability to mobilize body protein rapidly enough to provide sufficient amino acids for gluconeogenesis. Bouchat *et al.* (1980) have suggested that the immediately available labile protein reserve may play an important role as a glucogenic energy source during the interim period required for the mobilization of fatty acids and production of ketone bodies to reach a peak and stabilize following food deprivation. The importance of this mechanism is illustrated by results which show that sheep may loose up to 4% of total body protein within four days of fasting (Bouchat *et al.*, 1980). In this experiment, the acetate clearance rate test was used to examine the response to a sudden demand for glucose. The conversion of acetate to fatty acids is reliant on an adequate supply of NADPH, the production of which is thought to be largely dependent on glucose oxidation via the pentose–phosphate pathway in ruminants (Cronjé, 1990). As ruminants typically do not possess large glycogen reserves, the rate of clearance of an exogenous load of acetate would reflect the glucogenic potential of the diet and possibly also the ability of the animal to mobilize endogenous glucogenic precursors such as the labile protein reserves discussed above. Acetate clearance rate in sheep has been shown to increase with propionate and protein supplementation of roughage diets (Cronjé *et al.* 1992). The positive relationship between diet and acetate clearance observed in the present study is consistent with an increasing supply of dietary glucose precursors. There is also evidence to indicate that acetate clearance rate is influenced by the relative ability of the animal to mobilize endogenous sources of glucose. Several studies have shown that the addition of excess acetate to the diet is accompanied by increased nitrogen excretion (Tyrell *et al.*, 1979; Girdler *et al.* 1986); this is indicative of increased gluconeogenesis from amino acids. Pugh and Scarisbrick (1952) observed a reduced acetate clearance rate in ketotic ewes, suggesting that acetate clearance rate reflects the ability of the animal to mobilize

glucose precursors. The diagnostic significance of this test in the present context may be judged by the fact that the glucogenic challenge elicited by acetate loading was of sufficient magnitude to induce increased ketone concentrations in the sheep used by Jarrett *et al.* (1952). Although the consistently slower acetate clearance rate in Angora goats is indicative of a reduced capability to mobilize endogenous glucose precursors, a more severe reaction would have been expected in the case of adreno-cortical insufficiency. Alternatively, the slower acetate clearance rate may be a result of either an impaired ability to re-partition protein from hair synthesis to glucogenic pathways, or a smaller available labile protein reserve. This hypothesis is supported by previously reported results (Cronjé, 1992) which showed that nitrogen and urea were preferentially retained in the Angora goat vs. the Boer goat.

Conclusion

It has been suggested that the prime mediator of abortions, cold-related fatalities, and slow growth rates in the South African type of Angora goat is a condition of congenital adrenal insufficiency brought about by continued selection for increased hair production (Van Rensburg, 1971; Herselman, 1990). Although several lines of evidence discussed here (lower blood glucose concentration, larger volume of glucose distribution, slower increase in glucose flux rate with rising plane of nutrition, slower acetate clearance rate, higher nitrogen retention, lower urea excretion rate) are all consistent with an impaired gluconeogenic ability, no evidence could be found to indicate adrenal insufficiency as the cause. An alternative hypothesis is that selection for hair production alone has resulted in a shift in the partitioning of amino acids towards hair-protein synthesis and away from gluconeogenesis to the extent that the animal may be unable to mobilize sufficient labile protein reserves for glucose production during times of increased demand such as cold stress and pregnancy.

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