Glycolytic potential and ultimate muscle pH values in red deer (*Cervus elaphus*) and fallow deer (*Dama dama*)

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Abstract: The ultimate pH value of meat (measured at approx. 24 hours post slaughter) gives information about the technological quality, *i.e.* shelf life, colour, water-holding properties and tenderness and is a direct consequence of muscle glycogen (energy) levels at slaughter. It may therefore also indicate whether or not the animal has been exposed to stressful energy depleting events prior to slaughter. In the present study, 141 animals (130 red deer (*Cervus elaphus*) and 11 fallow deer (*Dama dama*) were included to investigate the relationship between ultimate pH and residual glycogen concentration in red deer and fallow deer *M. longissimus*. In addition, the muscle glycogen content and ultimate pH values in three red deer muscles (*Mm. triceps brachii, longissimus* and *biceps femoris*) were studied. *M. triceps brachii* had higher ultimate pH and lower glycogen content compared with the other two studied muscles. The frequency of intermediate DFD (5.8≤ pH<6.2) was 5.4% in red deer *M. longissimus*, compared with 9.1% in fallow deer, while the frequency of DFD (pH≥ 6.2) was much lower in red deer (3.8%) than in fallow deer (54.5%). A curvilinear relationship between ultimate pH and total glucose concentration (glycogen and glucose) 30 min post slaughter in red deer and fallow deer *M. longissimus* was found. The relationship between muscle pH and lactic acid concentration however, was indicated to be linear. A significant variation in total glucose concentration at ultimate pH below 5.80 was observed, including values in the range from 18 to 123 mmol/kg wet tissue. It was concluded that further studies are needed to further explore the relationship between muscle glycogen content and technological and sensory quality attributes of meat from different deer species.

Key words: DFD, glycogen, meat quality, nutritional status, pre-slaughter stress, venison.

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Introduction

New Zealand has pioneered the development of farm-based production systems for deer meat (venison) production. There are currently about 5000 deer farms in the country, ranging in size from smaller lifestyle properties to farms carrying thousands of deer. On these farms there are approximately 2 million deer, or half of the world's farmed deer population (Deer Industry New Zealand, 2003). Reflecting the original imported wild population, the majority of New Zealand's deer herd (about 85%) is red deer (*Cervus elaphus*). The balance of the national herd is predominantly elk (also known as wapiti or elk-wapiti) (*Cervus elaphus nelsoni*), which is descended from elk originally imported from Canada or red/elk hybrids. There are also small numbers of fallow deer (*Dama dama*). An important component of the research and development for the New Zealand deer industry has been to define production systems that give distinctive and high value attributes to venison, together with *post mortem* processing systems to complement these goals.

Muscle glycogen has been intensively studied because of its role in *in-vivo* stress, exercise-related energy metabolism and *post mortem* anaerobic glycolysis of muscle during *rigor mortis* development. The concentration of glycogen in muscle at the time

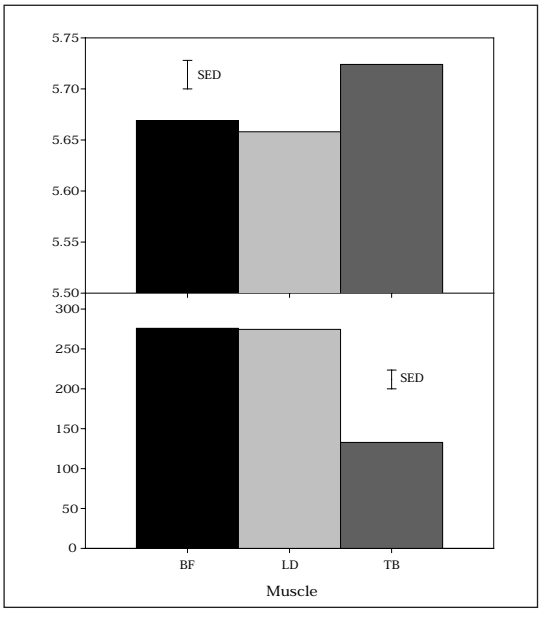

Fig. 1. Mean ultimate pH values and glycogen concentration (mmol/g dry tissue) in three muscles; *Mm. longissimus* (LD: ▫), *biceps femoris* (BF: ■) and *triceps brachii* (TB: ▪) from red deer (*Cervus elaphus*) (n=12). Bars indicate standard errors of difference (SED).

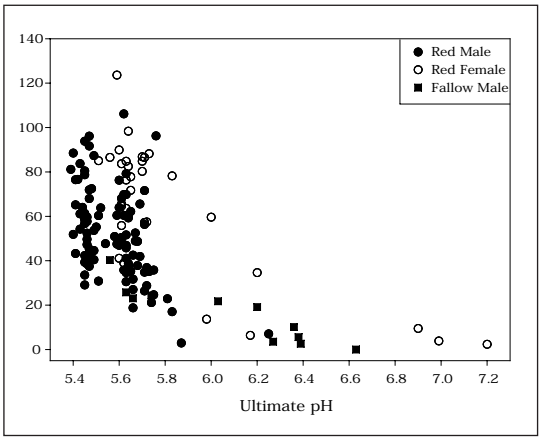

Fig. 2. The relationship between ultimate pH (24 h *post mortem*) and total glucose concentration (glycogen + glucose) at slaughter (30 min *post mortem*) in *M. longissimus* from male red deer (●; n=98), female red deer (○; n=32) and male fallow deer (■; n=11).

of slaughter is important because of its key role in preventing a quality defect known as dark-cutting or Dark, Firm, Dry (DFD). DFD meat has high ultimate pH values and short shelf life, especially for vacuum-packed meat (Gill & Newton, 1981). The high pH values also affect meat colour, texture and water-holding properties (Hood & Tarrant, 1981). Caused by a lack of normal acidification of meat during the development of *rigor mortis*, DFD is a direct consequence of low muscle glycogen at slaughter. Glycogen breakdown in muscle may be suddenly triggered by an increase in circulating adrenalin or by strenuous muscular activity (Tarrant, 1989). In monogastric animals the replenishment of glycogen in muscle is achieved in relatively few hours. Replenishment does not occur quite so readily in the muscles of ruminants because of the special ruminant carbohydrate metabolism, which has little direct access to dietary glucose and must rely on gluconeogenesis, in particular from propionate (Lister, 1989). High ultimate pH values in meat from ruminants (beef cattle, reindeer (*Rangifer tarandus tarandus*), red deer and fallow deer) have been related to pre-slaughter handling stress (Malmfors *et al*., 1983; Warriss *et al*., 1984; Warriss, 1990; Wiklund, 1996; Pollard *et al*., 1999) and poor nutritional status of the animals (Gregory, 1996; Wiklund *et al*., 1996; Pollard *et al*., 1999). Generally though, there is very limited basic information available on glycogen levels and metabolism in muscles and implications for meat quality for game animals like deer. In this study we present data from two of the most important deer species providing the world's bulk of venison; red deer (*C. elaphus*) and fallow deer (*D. dama*).

The purpose of this study was to investigate the relationship between ultimate pH and residual glycogen concentration in red deer and fallow deer *M. longissimus*. In addition, the muscle glycogen content and ultimate pH values in three red deer muscles (*Mm. triceps brachii, longissimus and biceps femoris*) were studied.

Material and methods

Animals

In total, 141 animals were included in the studies; 130 red deer (98 males and 32 females) and 11 male fallow deer. The animals were representative of normal variation in slaughter animals with respect to sex, age and physical condition (nutritional status, mainly the variation in fatness). All animals were exposed to normal pre-slaughter handling routines including yarding at the farm, short road transport (max. 1.5 h) and subsequent over-night lairage at the slaughter plant. The animals were slaughtered at Otago Venison Deer Slaughter Premises (Mosgiel, New Zealand) following a standard slaughter protocol. Ultimate pH and glycogen content were measured in *M. longissimus* from all 130 red deer and the 11 fallow deer (Fig. 2); 12 of the red deer (Group A) were selected for measurements of glycogen content and ultimate pH values in three muscles (*Mm. triceps brachii*, *longissimus* and *biceps femoris*) (Fig. 1). Another

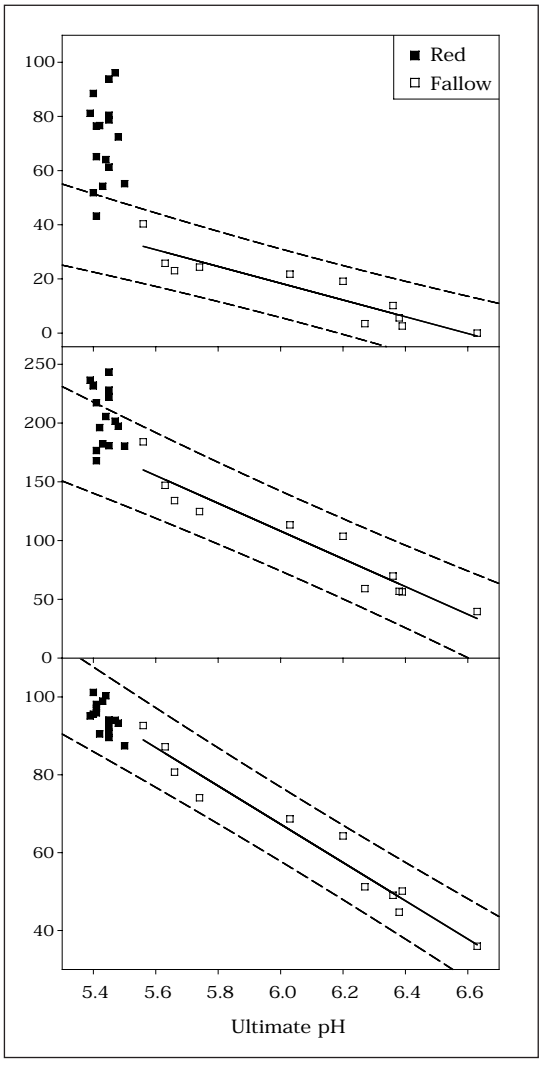

Fig. 3. The relationship between (a) total glucose concentration, (b) glycolytic potential and (c) lactate concentration and ultimate pH in *M. longissimus* from red deer (■; $n=16$) and fallow deer (□; $n=11$).

16 male red deer were selected for analysis of glycolytic potential in *M. longissimus* and compared with the 11 fallow deer (Group B) (Fig. 3).

Samples for glycogen determination were taken from the left side *Mm. longissimus* (LD) (at the last rib), *biceps femoris* (BF) and *triceps brachii* (TB) at 30 min *post mortem* and frozen in liquid nitrogen (–196 °C). At 1 day *post mortem*, pH values were measured in the LD (at the last rib), BF and TB and meat samples for analysis of glycolytic potential were collected from the LD and frozen at –80 °C.

pH measurements

For calibration of the pH equipment, buffers of pH 7.0 and 4.0 (Merck) at room temperature were used. When measuring the ultimate pH values (at approx. 24 h *post mortem*), muscle temperatures were also registered in order to adjust the pH meter accordingly. pH values were measured with a portable pH meter (Orion, model 265, Germany) equipped with a Xerolyte electrode (InLab®427, Mettler Toledo, Switzerland). Temperature was measured with a digital thermometer (Ebro, TFX 392 SK-S, Germany).

Glycogen determination in muscle samples

Muscle samples (1-2 g) were freeze-dried for 48 h. Connective tissue, fat and blood were removed under a dissection microscope, and glycogen analysed from the remaining tissue by assessing glucose residues after 15 mg of tissue had been boiled for 2 hr in 1 M HCl (Lowry & Passoneau, 1973).

Glycolytic potential

Glucose and glycogen were measured using a glucose oxidase assay (Trinder, 1969). Lactate was determined after deproteinising the tissue with 8% w/v perchloric acid followed by centrifugation at 1500g and +4° C for 15 minutes. Lactate was measured in the supernatant using a Sigma 826 UV kit (Sigma Diagnostic®, USA). The method used to analyse glucose-6-phosphate was based on oxidation to 6-phosphogluconolacetone by glucose-6-phosphate dehydrogenase, measuring the subsequent reduction of NADP (Lang & Michal, 1974).

Glycolytic potential (GP) was expressed in terms of potential lactate production according to the formula proposed by Monin and Sellier (1985), where brackets indicate concentration: GP = 2([glycogen] + [glucose] + [glucose-6-P]) + [lactate], expressed as micromoles of lactate equivalents per gram of fresh muscle.

Statistical analysis

Ultimate pH and glycogen values for Group A animals were analysed by ANOVA, with muscle within animal as the block structure and muscle as the treatment structure. The frequencies of intermediate DFD and DFD carcasses for all animals were analysed using a binomial generalized linear model with logit link function (McCullagh & Nelder, 1989), fitting species. Homogeneity of variance for total glucose concentration over DFD classes was tested using Bartlett's test (Snedecor & Cochran, 1980). Linear regression was used to model the relationship of total glucose concentration, glycolytic potential and lactic acid content to pH for fallow deer samples. Means of these variables for red and fallow deer in Group B were compared using *t*-tests, with separate variances for the two species groups. All analyses were conducted using GenStat (2002).

Table 1. Mean pH values (and standard deviation, except where noted) and the frequency of DFD (pH ≥ 6.2) and intermediate DFD (5.8 ≤ pH < 6.2) in *M. longissimus* from three deer species; red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and reindeer (*Rangifer tarandus tarandus*).

	Glycogen content (mmol/kg dry tissue)	Ultimate pH	Per cent intermediate DFD (5.8≤ pH<6.2)	Per cent DFD (pH≥ 6.2)
Red deer (*n*=130; this study)	210.7 (89.7)	5.64 (0.263)	5.4	3.8
Fallow deer (*n*=11; this study)	60.9 (47.9)	6.08 (0.372)	9.1	54.5
Red deer (*n*=3502)[1]	n.d.[3]	5.64 (0.158)	9.1	1.5
Fallow deer (*n*=104)[1]	n.d.	5.93 (0.196)	68.3	1.0
Reindeer (*n*=3400)[2]	n.d.	5.67 (5.670-5.674)[4]	23.1	6.0

[1] Pollard *et al*., 1999. [2] Wiklund *et al*, 1995. [3] n.d.= not determined.
[4] Back-transformed least squares means and ranges for means ± standard error of the mean (for further description, see Wiklund *et al*., 1995).

Results

Muscle pH values, glycogen content and frequency of DFD carcasses

Ultimate pH values did not differ significantly between the three measured red deer muscles, although the mean value for *M. triceps brachii* (5.72) was significantly higher than the combined mean of *Mm. longissimus* and *biceps femoris* (5.66; Standard Error of Difference (SED) 0.024). Further, *M. triceps brachii* had lower ($P<0.001$) glycogen levels than either of the other two muscles (Fig. 1).

The frequency of intermediate DFD (5.8≤ pH<6.2) was 5.4% in red deer *M. longissimus*, compared with 9.1% (SED 8.9; $P>0.05$) in fallow deer, while the frequency of DFD (pH≥ 6.2) was much lower in red deer (3.8%) than in fallow deer (54.5 % (SED 15.1); $P<0.001$) (Table 1).

Total glucose concentration at slaughter 30 min post mortem*, glycolytic potential and lactic acid content*

Total glucose concentration (free glucose + glycogen) is plotted against ultimate pH (*M. longissimus*) in Fig. 2, and summarised by DFD status in Table 2. There was evidence of inhomogeneity of variance ($P<0.05$) over the DFD classes. For carcasses with ultimate pH below 5.8 both the mean and standard deviation for glucose concentration were high (range 18.8 to 123.6 mmol/kg), while for carcasses in the DFD- group both the mean and standard deviation were low (range 0.0 - 34.6 mmol/kg). In the intermediate group the carcasses had intermediate mean values for total glucose concentration and a high standard deviation (Table 2).

Total glucose concentration, glycolytic potential and lactic acid content were plotted against ultimate pH in *M. longissimus* for 16 of the male red deer carcasses and the 11 fallow deer in Fig. 3, with summary statistics presented in Table 3. For the red deer ultimate pH covered a narrow range (5.39-5.50), in contrast to the wide range for fallow deer (5.56-6.63). For fallow deer regression lines with 95% confidence bands were fitted against pH, with 1, 9 and 16 red deer falling within these bands for total glucose, glycolytic potential and lactic acid, respectively (Fig. 3).

Discussion

The pre-slaughter handling of animals has an important effect on the quality of meat as well as implications for animal welfare (Warriss, 1993; Gregory, 1996; Goddard, 1998). When animals are subjected to stress, their muscle glycogen stores can become depleted, which will result in high ultimate pH values in the meat (DFD). There are numerous reports that variation in muscle pH and glycogen content gives rise to considerable variations in meat tenderness in species such as beef and lamb (*e.g.* Smulders *et al*., 1990; Devine, 1994; Watanabe *et al*., 1996). Within the normal range (non-DFD) for ultimate pH in beef and red deer *M. longissimus*, values around 5.5 have been reported to yield more tender meat than in the 5.8-6.0 range (Purchas, 1990; Jeremiah *et al*., 1991; Barnier *et al*., 1992; Stevenson-Barry *et al*., 1999). In a red deer study (Stevenson-Barry *et al*., 1999) it was indicated that the tenderness profile change after ageing at 4 °C was similar to that reported for lamb, in that all LD samples tenderised to an acceptable level. However, the intermediate pH (5.8-6.0) meat still tended to be tougher than the normal pH meat and was more variable in tenderness (*i.e.* less consistent quality) than normal pH meat (Stevenson-Barry *et al*., 1999). In contrast, reindeer LD was found to be extremely tender regardless of ultimate pH (Wiklund *et al*., 1997) and ultimate tenderness was almost reached at 3 days *post mortem*. In a recent study it was indicated that the tenderness

Table 2. Mean values and standard deviation (*s*) for total glucose concentration (mmol/kg) in *M. longissimus* from red deer and fallow deer carcasses (in total 141 animals) classified in three pH groups.

Ultimate pH	*n*	Total glucose concentration (mmol/kg)	*s*
pH < 5.8	122	57.9	21.1
5.8 ≤ pH ≤ 6.2	8	27.8	26.7
pH ≥ 6.2	11	8.9	10.0

development in fallow deer LD was similar to that of reindeer, producing tender meat as early as 2-3 days *post mortem* (Sims *et al*., 2004). In a survey of pre-slaughter handling and post-slaughter meat quality variables at a commercial deer slaughter plant in the South Island of New Zealand, data from 3,606 animals (red deer and fallow deer) were analysed (Pollard *et al*., 1999). The frequency of DFD ($pH_u \geq 6.2$ in *M. longissimus*) in red deer and fallow deer in this study (Pollard *et al*., 1999) was low (1.5 and 1 % respectively) compared with earlier studies on reindeer, where 6% of the carcasses were classified as DFD (Wiklund *et al*., 1995). The present results showed a higher percentage of DFD and a lower percentage of intermediate DFD (5.8≤pH<6.2) carcasses for both red deer and fallow deer (Table 1) compared with the previously mentioned deer survey. In conclusion, the present results showed – in good agreement with previously mentioned deer and reindeer studies – that there are possibly several pre-slaughter conditions (*e.g.* handling routines and nutritional status) that could be improved for deer and reindeer, which would lead to a more consistent venison quality. The pre-slaughter handling procedures used for reindeer in Scandinavia and for farmed red deer and fallow deer in New Zealand are very similar and a collaborative approach to further research would therefore be useful.

However, it is important to note that the history of reindeer husbandry in Scandinavia and that of deer farming in New Zealand is quite different. Reindeer have been managed as semi-domestic animals probably for thousands of years, and individual animals which have been difficult to handle or easy to stress have been selected against. Intensive deer farming in New Zealand is a new industry, so the same selection procedure on animal temperament has not come so far yet. One might also speculate that there are genetic differences in temperament and manageability between the three species (reindeer, red deer and fallow deer), which could influence ultimate muscle pH values and DFD frequencies. Pollard *et al.* (1999) specifically referred to stressed animals and difficulties in managing fallow deer during transport, over-night lairage at the slaughter plant and during stunning when explaining the high frequency of intermediate DFD (68.3%; see Table 1) for this species. Natural variation in body condition could also explain the higher frequency of DFD in reindeer compared with the other two deer species. All three deer species have a seasonal growth pattern regulated by day length, where reindeer in the Northern hemisphere are exposed to a more extreme variation in long dark and light periods over the year compared with farmed deer in New Zealand. Also, reindeer are managed in a free ranging system totally dependent on natural pastures in a very harsh environment. Therefore, the annual variation in body condition, and thereby in muscle glycogen levels, could be expected to be more marked in reindeer than in the two other deer species managed in an intensive farming system on cultivated pastures.

The variation in ultimate pH between different muscles reported for several species is probably due to the way in which the muscle is affected by physical activity, and also by the fibre type distribution within the muscle. A large proportion of oxidative (types I and IIa) fibre types in beef *M. longissimus* gave high ultimate pH values and increased the incidence of DFD (Zerouala & Stickland, 1991). In cattle, during physical activity, working muscles became selectively depleted in glycogen and within these muscles the fast-twitch fibres (types IIa and IIb) were affected (Tarrant, 1989). On the other hand, in bovine slow-twitch fibres (type I) adrenaline release due to emotional stress caused a greater loss of glycogen, indicating that muscles containing a large proportion of slow-twitch fibres would become more glycogen depleted following emotional stress (Tarrant, 1989). In reindeer, ultimate pH values in different muscles have been compared and generally shoulder muscles have been found to have higher pH values than, *e.g.*, *M. longissimus* and various leg muscles like *M. biceps femoris* and *M. semimembranosus* (Skjenneberg *et al*., 1974; Petäjä, 1983; Wiklund *et al*., 1995). Smoked reindeer shoulder is a valuable traditional product and high pH values would make the meat less suitable for smoking (Niinivaara & Petäjä, 1984); therefore it was concluded that the observed high ultimate pH values in *M. triceps brachii* might affect its applicability (Wiklund, 1996). The results from the present study are in good agreement with the previously mentioned reindeer studies, since the red deer *M. triceps brachii* had higher ultimate pH value and lower glycogen content than the other two studied muscles (*Mm. longissimus* and *biceps femoris*). It is reasonable to

Table 3. Mean values (with ranges bracketed) for ultimate pH, total glucose concentration, glycolytic potential and lactic acid concentration in *M. longissimus* from male red deer (n=16) and fallow deer (n=11) included in the study, with standard errors of difference (SED) based on separate variances for each species.

	Red deer (n=16)	Fallow deer (n=11)	SED	Degree of significance[1]
Ultimate pH	5.44 (5.39-5.50)	6.08 (5.56-6.63)	0.11	***
Total glucose (mmol/kg)	71.2 (43.2-96.1)	16.0 (0.0-40.3)	5.43	***
Glycolytic potential (mmol/kg)	206.2 (167.9-243.3)	98.9 (39.6-184.0)	15.2	***
Lactic acid (mmol/kg)	94.6 (87.5-101.2)	63.5 (36.0-92.7)	5.7	***

[1] *** means $P \leq 0.001$.

believe that red deer in the present study reacted in a similar way to the pre-slaughter handling procedures that was suggested for reindeer (Wiklund, 1996), so that the mixture of both physical and emotional stress events more seriously affected muscles containing a large proportion of slow-twitch fibres (like the *M. triceps brachii*). Reindeer *M. triceps brachii* has been found to contain 30-40% slow-twitch fibres (Essén-Gustavsson & Rehbinder, 1985). For the deer industries it is important to recognise the demonstrated quality differences between various muscles within the carcass, as well as to acknowledge the importance of minimal stress exposure during pre-slaughter handling of animals. These measures will safeguard meat quality, animal welfare and produce raw material of good quality for further processing.

In animals in good physical condition, the muscles contain enough glycogen to guarantee optimal ultimate pH values in the meat. Red deer glycogen values in the range of 120 to 220 mmol/kg dry tissue in *M. splenius* and *M. longissimus* have been reported (Wiklund *et al*., 2001; Pollard *et al*., 2002; Wiklund *et al*., 2003). These values were generally lower than those found in other species like pig, horse and cattle (*e.g.* Lindholm *et al*., 1974; Immonen *et al*., 2000a; Rosenvold *et al*., 2002), but similar to glycogen values found in reindeer slaughtered directly from pasture during winter (Wiklund *et al*., 1996). To feed reindeer with grain-based pellets for 2 months prior to slaughter has been shown to improve the nutritional status and increase muscle glycogen stores, so that fed animals had glycogen values comparable with those found in cattle (Wiklund *et al*., 1996). The glycogen values registered in red deer samples in the present study are in good agreement with the previously mentioned deer studies. The present results for glycolytic potential and lactic acid concentration in the red deer and fallow deer samples fell into the ranges earlier reported for beef (Daly *et al*., 1999; Immonen & Puolanne, 2000). Immonen & Puolanne (2000) described a curvilinear relationship between ultimate pH and residual carbohydrate (glycogen + glucose at 48 h post slaughter) concentration in beef *Mm. longissimus, gluteus medius* and *semimembranosus,* while the relationship between muscle pH and lactic acid concentration was linear. The same authors also reported a very big variation in residual carbohydrate levels (from 10 to 83 mmol/kg wet tissue) at low muscle pH. Similar results were found in the present study with a negative association between ultimate pH and total glucose concentration (glycogen and glucose) 30 min post slaughter in red deer and fallow deer *M. longissimus* (Fig. 2). The relationship between muscle pH and lactic acid concentration in the present study was indicated to be linear, although the limited variation in pH in the red deer samples made this correlation somewhat unclear (Fig. 3). The variation in total glucose concentration at ultimate pH below 5.80 in the present study was significant, including values in the range from 18 to 123 mmol/kg wet tissue (Fig. 2). Also in good agreement with Immonen & Puolanne (2000), we observed some total glucose concentrations at higher pH values in red deer and fallow deer *M. longissimus* that would have been sufficient to cause an additional pH fall, but for some reason this did not occur. The independent effects of residual glycogen concentration on the physical and sensory quality of normal-pH beef were investigated by Immonen *et al*. (2000b). An increasing concentration of residual glycogen was reported to improve both water holding capacity (measured as drip loss) and tenderness of the meat, although these effects were moderate in size. In the present study, no similar evaluation of the effects of glycogen content on various meat quality traits was performed. The relationship between muscle glycogen content and technological and sensory quality attributes of venison from different deer species is of great interest for further research.

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References

Barnier, V. M. H., Geesink, G. H., Smulders, F. J. M. and van Logtestijn, J. G. 1992. Rate of glycolysis, chilling rate and beef quality: an inventory of potential consequences. – *In: Proceedings: 38th International Congress of Meat Science and Technology*, Clermont-Ferrand, France, pp. 321-324.

Daly, C. C., Young, O. A., Graafhuis, A. E. & Moorhead, S. M. 1999. Some effects of diet on beef meat and fat attributes. – *New Zealand Journal of Agricultural Research* 42: 279-287.

Deer Industry New Zealand. 2003. Internet homepage: Available at: http://www.deernz.org

Devine, C. E. 1994. Incidence of high pH beef and lamb. I: implications for meat quality. – *In: Proceedings: 28th Meat Industry Research Conference*, Auckland, New Zealand, pp. 125-132.

Essén-Gustavsson, B. & Rehbinder, C. 1985. Skeletal muscle characteristics of reindeer (*Rangifer tarandus* L). – *Comparative Biochemistry and Physiology* 82A: 675-679.

Genstat 5 Committee. 2002. *GenStat for Windows (Sixth Edition)*. VSN International, Oxford.

Gill, C. O. & Newton, K. G. 1981. Microbiology of DFD beef. – *In*: D. E. Hood & P. V. Tarrant (eds.). *The problem of Dark-cutting in Beef*. Martinus Nijhoff, Den Haag, pp. 305-327.

Goddard, P. J. 1998. The welfare of deer. – *Acta Veterinaria Hungarica* 46: 395-404.

Gregory, N. G. 1996. Welfare and hygiene during preslaughter handling. – *Meat Science* 43S: S35-S46.

Hood, D. E. & Tarrant, P. V. 1981. *The problem of Dark-cutting in Beef*. Martinus Nijhoff, Den Haag.

Immonen, K. & Puolanne, E. 2000. Variation of residual glycogen-glucose concentration at ultimate pH values below 5.75. – *Meat Science* 55: 279-283.

Immonen, K., Ruusunen, M., Hissa, K. & Puolanne, E. 2000a. Bovine muscle glycogen concentration in relation to finishing diet, slaughter and ultimate pH. – *Meat Science* 55: 25-31.

Immonen, K., Ruusunen, M. & Puolanne, E. 2000b. Some effects of residual glycogen concentration on the physical and sensory quality of normal pH beef. – *Meat Science* 55: 33-38.

Jeremiah, L. E., Tong, A. K. W. and Gibson, L. L. 1991. The usefulness of muscle colour and pH for segregating beef carcasses into tenderness groups. – *Meat Science* 30: 97-114.

Lang, G. & Michal, G. 1974. *In*: H. Bergmeyer (ed.). *Methods of enzymatic analysis*, 2nd edition. Academic Press, N. Y.

Lindholm, A., Bjernseld, H. & Saltin, B. 1974. Glycogen depletion pattern in muscle fibres of trotting horses. – *Acta Physiologica Scandinavia* 90: 475-484.

Lister, D. 1989. Muscle metabolism and animal physiology in the dark cutting condition. – *In*: S. U. Fabiansson, W. R. Shorthose & R. D. Warner (eds.). *Dark-cutting in cattle and sheep. Proceedings of an Australian workshop.* Australian Meat & Livestock Research & Development Corporation, Sydney, Australia, pp. 19-25.

Lowry, O. H. & Passoneau, J. V. 1973. *A flexible system for enzymatic analysis*. Academic Press, New York.

Malmfors, G., Lundström, K. & Fabiansson, S. 1983. Influence of handling systems on meat quality of beef. – *In: Proceedings '29th European Congress of Meat Research Workers'*, Salsomaggiore, Italy, pp. 70-75.

McCullagh, P. & Nelder, J. A. 1989. *Generalized linear models (second edition)*. Chapman and Hall, London.

Monin, G. & Seller, P. 1985. Pork of low technological quality with a normal rate of muscle pH fall in the immediate post mortem period: the case of the Hampshire breed. – *Meat Science* 13: 49-63.

Niinivaara, F. P. & Petäjä, E. 1984. Problems in the production and processing of reindeer meat. – *In:* Krol, B., van Roon, P. S. & Houben, J. H. (eds.). *Trends in modern meat technology*. Pudoc, Wageningen, The Netherlands, pp. 115-120.

Petäjä, E. 1983. DFD meat in reindeer meat. – *In: Proceedings: 29th European Congress of Meat Research Workers*, Salsomaggiore, Italy, pp. 117-124.

Pollard, J. C., Littlejohn, R. P., Asher, G. W., Pearse, A. J. T., Stevenson-Barry, J. M., McGregor, S. K., Manley, T. R., Duncan, S. J., Sutton, C. M., Pollock, K. L. & Prescott, J. 2002. A comparison of biochemical and meat quality variables in red deer (*Cervus elaphus*) following either slaughter at pasture or killing at a deer slaughter plant. – *Meat Science* 60: 85-94.

Pollard, J. C., Stevenson-Barry, J. M. & Littlejohn, R. P. 1999. Factors affecting behaviour, bruising and pH_u in a deer slaughter premises. – *In: Proceedings: New Zealand Society of Animal Production*, pp. 148-151.

Purchas, R. W. 1990. An assessment of the role of pH differences in determining the relative tenderness of meat from bulls and steers. – *Meat Science* 27: 129-140.

Rosenvold, K., Lærke, H. N., Jensen, S. K., Karlsson, A. H., Lundström, K. & Andersen, H. J. 2002. Manipulation of critical quality indicators and attributes in pork through vitamin E supplementation, muscle glycogen reducing finishing feeding and preslaughter stress. – *Meat Science* 62: 485-496.

Sims, K. L., Mulley, R. C., Hutchison, C. L. & Wiklund, E. 2004. Post slaughter management of fallow deer (*Dama dama*) – Effect of pelvic suspension method on meat tenderness. – *In: Proceedings Australian*

Deer Industry Biennial Conference, 16-18 April, Mt Gambier, Australia.

Skjenneberg, S., Jacobsen, E. & Movinkel, H. 1974. pH-verden i reinkjøtt etter forskjellig behandling av dyrene for slakting (pH values in reindeer meat after different pre-slaughter handling of the animals). – *Nordisk Veterinärmedicin* 26: 436-443 (in Norwegian).

Smulders, F. J. M., Marsh, B. B., Swartz, D. R., Russell, R. L. & Hoenecke, M. E. 1990. Beef tenderness and sarcomere length. – *Meat Science* 28: 349-363.

Snedecor, G. W. & Cochran, W. G. 1980. *Statistical Methods* (7th Edition), Iowa State University Press, Ames, Iowa.

Stevenson-Barry, J. M., Carseldine, W. J., Duncan, S. J. & Littlejohn, R. P. 1999. Incidence of high pH venison: implications for quality. – *In: Proceedings: New Zealand Society of Animal Production* 59, pp. 145-147.

Tarrant, P. V. 1989. Animal behaviour and environment in the dark-cutting condition in beef – a review. – *Irish Journal of Food Science and Technology* 13: 1-21.

Trinder, P. 1969. Determination of glucose in blood using Glucose Oxidase with an alternative oxygen acceptor. – *Annual Clinical Biochemistry* 6: 24-27.

Warriss, P. D. 1990. The handling of cattle pre-slaughter and its effect on carcass and meat quality. – *Applied Animal Behaviour Science* 28: 171-186.

Warriss, P. D. 1993. Ante-mortem factors which influence carcass shrinkage and meat quality. – *In: Proceedings: 39th International Congress of Meat Science and Technology*, Calgary, Canada, pp. 51-65.

Warriss, P. D., Kestin, S. C., Brown, S. N. & Wilkins, L. J. 1984. Time required for recovery from mixing stress in young bulls and the prevention of dark cutting beef. – *Meat Science* 10: 53-68.

Watanabe, A., Daly, C. C. & Devine, C. E. 1996. The effects of ultimate pH of meat on tenderness changes during ageing. – *Meat Science* 42: 133-144.

Wiklund, E. 1996. *Pre-slaughter handling of reindeer – effects on meat quality*. Dr. thesis, Department of Food Science, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Wiklund, E., Andersson, A., Malmfors, G. & Lundström, K. 1996. Muscle glycogen levels and blood metabolites in reindeer (*Rangifer tarandus tarandus* L) after transport and lairage. – *Meat Science* 42: 133-144.

Wiklund, E., Andersson, A., Malmfors, G., Lundström, K. & Danell Ö. 1995. Ultimate pH values in reindeer meat with particular regard to animal sex & age, muscle and transport distance. – *Rangifer* 15: 47-54.

Wiklund, E., Barnier, V. M. H., Smulders, F. J. M., Lundström, K. & Malmfors, G. 1997. Proteolysis and tenderisation in reindeer (*Rangifer tarandus tarandus* L) bull longissimus thoracis muscle of various ultimate pH. – *Meat Science* 46: 33-43.

Wiklund, E., Manley, T. R., Littlejohn, R. P. & Stevenson-Barry, J. M. 2003. Fatty acid composition and sensory quality of *Musculus longissimus* and carcass parameters in red deer (*Cervus elaphus*) grazed on natural pasture or fed a commercial feed mixture. – *Journal of the Science of Food and Agriculture* 83: 419-424.

Wiklund, E., Stevenson-Barry, J. M., Duncan, S. J. & Littlejohn, R. P. 2001. Electrical stimulation of red deer (*Cervus elaphus*) carcasses – effects on rate of pH-decline, meat tenderness, colour stability and water holding capacity. – *Meat Science* 59: 211-220.

Zerouala, A. C. & Stickland, N. C. 1991. Cattle at risk for dark-cutting beef have a higher proportion of oxidative muscle fibres. – *Meat Science* 29: 263-270.

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Abstract in Swedish / Sammanfattning:

Köttets pH-värde (mätt *ca* 24 timmar efter slakt) har stor betydelse för den teknologiska kvaliteten som t. ex. hållbarhet, färg, vattenhållande förmåga och mörhet. Glykogenförrådet (energinivån) i djurens muskulatur vid slakt är helt avgörande för köttets slutliga pH-värde. Därför kan pH-värdet också indikera om hanteringen av slaktdjur varit skonsam eller om stora mängder muskelenergi har förbrukats vid stress. I vår undersökning ingick 141 hjortar (130 kronhjortar (*Cervus elaphus*) och 11 dovhjortar (*Dama dama*) för att studera sambandet mellan köttets pH-värde och glykogeninnehållet i *M. longissimus*. Glykogeninnehåll och pH-värden i 3 muskler från kronhjort (*Mm. triceps brachii, longissimus och biceps femoris*) undersöktes också. *M. triceps brachii* hade högre pH-värde och lägre glykogeninnehåll jämfört med de två andra musklerna. Det var inte så stor skillnad i frekvensen av intermediär DFD (pH-värden mellan 5,8 og 6,2) mellan de två hjortarterna (5,4% för kronhjort och 9,1% för dovhjort), däremot var frekvensen av DFD (pH-värden över 6,2) mycket låg hos kronhjort (3,8%) jämfört med dovhjort (54,5%). Det fanns ett kurvlinjärt samband mellan slutligt pH-värde i köttet och total glukoskoncentration (glykogen + glukos) mätt i *M. longissimus* 30 min efter slakt för både kron- och dovhjort. Ett linjärt samband mellan pH-värde och koncentration av mjölksyra i *M. longissimus* kunde också visas. Vi fann en mycket stor varitation i glukoskoncentration (18–123 mmol/kg våtvikt) när köttets pH-värdet var 5,8 eller lägre. Det behövs fler undersökningar för att vidare klargöra sambanden mellan glykogeninnehåll i muskulaturen och teknologisk och sensorisk kvalitet i olika typer av hjortkött.