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Comparison of glutathione peroxidase activity, and of total and soluble selenium content in two muscles from chicken, turkey, duck, ostrich and lamb

Charlotte Daun, Björn Åkesson*

Biomedical Nutrition, Lund Institute of Technology, Lund University, PO Box 124, SE-221 00, Lund, Sweden

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Abstract

Glutathione peroxidase activity (GSHPx), total and soluble selenium in two muscles from five species were compared (chicken, duck, turkey, ostrich and lamb). The highest GSHPx activity, found in duck muscles (4.8 U/g; 3.0 U/g), was significantly higher than that in lamb (1.8 U/g; 1.4 U/g), turkey (1.2 U/g; 0.6 U/g), chicken (1.0 U/g; 0.7 U/g), and ostrich muscles (0.9 U/g; 0.8 U/g). GSHPx activities were significantly higher in the oxidative muscles from chicken (thigh), duck (breast), turkey (thigh) and lamb (PM) than those in the corresponding glycolytic muscles (breast, thigh, breast and LD, respectively). Also the total selenium content was higher in duck muscles (149 ng/g; 139 ng/g), than in lamb (171 ng/g /PM, *M. psoas major*/ and 86 ng/g /LD, *M. longissimus dorsi*/), chicken (117 ng/g; 109 ng/g), ostrich (106 ng/g; 103 ng/g) and turkey muscles (110 ng/g; 70 ng/g). The selenium content was significantly higher in the oxidative muscles of lamb and turkey than in the corresponding glycolytic muscles. The percentage of soluble selenium in lamb PM was lower (32%) than that in all other muscles (range 48–76%). The study thus showed considerable variation, among species, of glutathione peroxidase activity, total and soluble selenium content in muscle, which may be important for the oxidative stability and nutritional value of different meat products.
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Keywords: Glutathione peroxidase; Selenium; Lipid oxidation; Meat quality; Chicken; Turkey; Duck; Ostrich; Lamb

1. Introduction

In Sweden, meat constitutes an important source of selenium for humans with an average contribution of 21% to the selenium intake (Becker, 2000). Most of the meat is consumed as pork (15 kg/person and year), followed by beef (11 kg/person and year), and during the 1990s the consumption of poultry increased to 12 kg/person and year. A relatively new kind of meat on the Swedish market is ostrich, which has a more beneficial nutritional composition with a lower fat-to-protein ratio and cholesterol content than beef (Paleari et al., 1998).

Deteriorative oxidative reactions in meat lead to losses of both nutritional value and food quality. Endogenous antioxidants control the oxidation in muscle tissue, e.g. α-tocopherol, ubiquinone, histidine-containing dipeptides and such antioxidative enzymes as superoxide dismutase, catalase and glutathione peroxidase (GSHPx) (Chan & Decker, 1994; Decker, Livisay, & Zhou, 2000). To increase the oxidative stability of meat, antioxidants have been added to the feed of farm animals, leading to an improved meat quality, especially using vitamin E (Lauridsen, Krogh Jensen, Skibsted, & Bertelsen, 2000; Lynch, Kerry, Buckley, Faustman, & Morrissey, 1999). In several studies, supplementation of the feed with selenium was found to decrease lipid oxidation in chicken meat (Combs & Regenstein, 1980; DeVore, Colnago, Jensen, & Greene, 1983) but not in beef (O'Grady, Monahan, Fallon, & Allen, 2001).

Selenium is an essential trace element, which is important for both human and animal health. Meat, fish, milk and egg are foods rich in selenium, although their selenium contents and thus the total selenium intake vary widely between countries. Most of the sele-

* Corresponding author. Tel.: +46-46-222-95-81; fax: +46-46-222-38-53.

E-mail address: bjorn.akesson@kc.lu.se (B. Åkesson).

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nium in mammalian tissues is associated with the amino acids selenocysteine and selenomethionine in proteins. Important specific selenoproteins are the glutathione peroxidases (E.C. 1.11.1.9), having antioxidative action and contributing to the oxidative defence by catalysing the reduction of hydrogen and lipid peroxides to less harmful hydroxides (Arthur, 2000; Burk, 1997). The mammalian glutathione peroxidase family consists of at least four selenoproteins: cellular, extracellular, phospholipid hydroperoxide, and gastrointestinal GSHPx (Arthur, 2000; Ursini et al., 1995). Many other selenoproteins have been found in mammals (Köhrle et al., 2000), but little is known of their importance for food quality, e.g. in different meats.

Muscle fibres can be categorized into different metabolic types: oxidative (red) or glycolytic (white), based on their chemical composition and enzyme activities (Lawrie, 1979). The oxidative muscles have more mitochondria and a higher content of myoglobin than the glycolytic ones. They mainly use fatty acids as substrates and have low activities of ATPase and phosphorylase, while the glycolytic muscles use mainly glycogen as an energy source and have higher activities of the latter enzymes. Chicken and turkey breast muscles are considered white whereas their thigh muscles are red but other birds, such as ducks, have the opposite distribution of white and red meat between these two muscles. Previous studies have shown a higher GSHPx activity in oxidative (thigh) than in glycolytic (breast) muscles of chicken and turkey (DeVore et al., 1983; Lee, Mei, & Decker, 1996).

The aim of this paper was to compare the GSHPx activity, and total and soluble selenium in two different muscles from five species used as human foods, namely chicken, turkey, duck, ostrich and lamb. No previous study has compared the GSHPx activity from these species using the same method for activity analysis. Another interesting variable for the understanding of the role of selenium compounds in meat is the proportion of soluble selenium content, and such data are only available for beef and pork (Daun, Johansson, Önning, & Åkesson, 2001).

2. Materials and methods

2.1. Chemicals

Hydrochloric acid, nitric acid and perchloric acid were of pure analytical grade. *t*-Butyl hydroperoxide and glutathione reductase were purchased from Merck (Darmstadt, Germany) and Boehringer Mannheim (Germany), respectively. Glutathione, NADPH and mercaptosuccinate were purchased from Sigma Chemical Co (St. Louis, USA). Other chemicals were of reagent grade.

2.2. Selenium content of feed

Samples of the feed given to chicken, duck and turkey were collected at the breeding houses, and stored at room temperature. The feed differed during various phases of breeding. The samples were subjected to selenium analysis.

2.3. Meat sources

All muscle samples were obtained from local slaughterhouses, except for lamb that was purchased at a local butcher. The chickens, ducks and turkeys were slaughtered at the age of 35, 56 and 140 days, respectively. Chicken, duck and turkey muscles [*m. pectoralis* (breast), *m. gastrocnemius* and *m. peroneus longus* (thigh)], ostrich (steak and fillet) and lamb muscles [*m. longissimus dorsi* (LD), *m. psoas major* (PM)] were frozen at −20 °C. Each pair of muscles was taken from the same animal ($n = 5$). Breast from chicken and turkey, thigh from duck, and LD from lamb were considered as glycolytic muscles, and the other muscles from those species as oxidative.

2.4. Sample preparation

After thawing, the meat samples were kept on ice during the procedure. All visible fat was removed prior to grinding the meat through a plate with holes 6 mm in diameter. Samples were then diluted (1:4) with cold potassium phosphate buffer (80 mmol/l) containing 5 mmol/l of EDTA, 2 mmol/l of glutathione (pH 7.6) and homogenised in an Ultra Turrax apparatus for 20 seconds at maximum speed. After centrifugation at 5000 *g* for 20 min (4 °C) (Beckman GPR), the supernatant was filtered and frozen at −70 °C.

2.5. Glutathione peroxidase activity

The activity of glutathione peroxidase was measured in the supernatants by a coupled assay procedure (Chen, Lindmark Månsson, & Åkesson, 2000) as adapted for meat analysis (Daun et al., 2001), recording the oxidation of NADPH by the decrease in absorbance at 340 nm. The assay mixture contained *tert*.butyl hydroperoxide (0.10 mmol/l), glutathione (0.63 mmol/l), NADPH (0.25 mmol/l), EDTA (5 mmol/l), and glutathione reductase (5 μg/ml) in potassium phosphate buffer (50 mmol/l; pH 7.6). To control for possible interfering activity from other NADPH-oxidizing enzymes a blank was run for every type of sample, consisting of the complete incubation mixture plus mercaptosuccinate (4 mmol/l), an inhibitor of GSHPx (Chaudiere, Wilhelmsen, & Tappel, 1984). Treatment of the ostrich samples with mercaptosuccinate revealed an approximately twice higher blank value in the fillet

samples than a water blank, indicating presence of other NADPH oxidizing enzymes. A mercaptosuccinate-containing blank was therefore used for all ostrich samples. The GSHPx activity in meat was expressed as U/g (wet weight), where one unit (U) was defined as 1 μmol oxidized NADPH/min. A serum control was included in every assay.

2.6. Selenium analysis

The selenium content was measured using hydride generation graphite furnace atomic absorption spectrometry (HG-GF-AAS; Perkin Elmer Aanalyst 800) combined with flow injection analysis (FIAS-400), according to the method previously described (Daun et al., 2001). Bovine liver (NIST 1577b) or bovine muscle (CRM 184) was included as a reference material in every assay. The imprecision, expressed as the inter- and intra-assay coefficient of variation, was 2.8 and 3.5%, respectively.

2.7. Statistical analysis

For comparison of data obtained in two muscles from the same species, the paired *t*-test was used. One-way ANOVA, followed by Tukey's test, was used to assess the significance of differences between groups. Linear correlation coefficients were computed.

3. Results

3.1. Glutathione peroxidase activity

The activity of GSHPx varied more than 5-fold among the muscles from different species (Fig. 1). The highest activity, found in duck muscles, was significantly higher than that in all other muscles ($P<0.001$; vs lamb PM $P<0.01$). Moreover, lamb PM had a significantly higher GSHPx activity than chicken and turkey breast ($P<0.01$) and ostrich fillet ($P<0.05$). Another interesting comparison to make was that between oxidative and glycolytic muscles for each species. In the oxidative muscles of chicken, duck, lamb and turkey, GSHPx activities were significantly higher than those of the glycolytic muscles (Fig. 1).

3.2. Total selenium content

The muscle selenium content varied only approximately 2-fold among species (Fig. 2). Significantly higher total selenium content was found in lamb PM than in all other muscles except for duck breast, which in turn contained significantly more selenium than chicken breast ($P<0.01$) and thigh ($P<0.05$), both turkey muscles ($P<0.01$) and ostrich muscles ($P<0.01$) and lamb LD ($P<0.001$). The lowest content of selenium was found in turkey breast ($P<0.05$–$P<0.001$ vs. other bird muscles). With respect to the comparison between oxidative and glycolytic muscles, significantly higher total selenium content was found in oxidative muscles of lamb and turkey than in the corresponding glycolytic ones (Fig. 2).

3.3. Content of soluble selenium in muscle

Since GSHPx is a soluble selenoprotein it was pertinent also to study the content of soluble selenium in the muscles. Considering the high total selenium content in lamb PM, it was an interesting finding that its percentage of soluble selenium (32%) was much lower than that of the other muscles, ranging from 48% in turkey breast to 76% in chicken thigh (Table 1). The soluble selenium content (ng/g) in oxidative muscles from chicken, turkey and duck was significantly higher than that in the corresponding glycolytic ones, and a similar tendency was found in lamb muscles (Table 1).

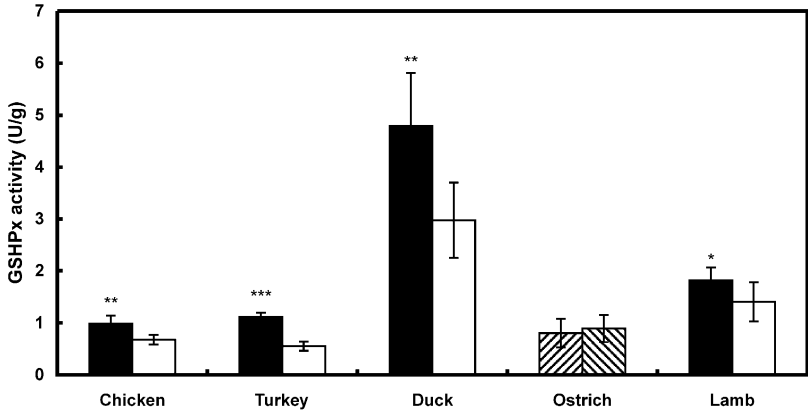

Fig. 1. Glutathione peroxidase activity (U/g) in breast and thigh muscles from chicken, duck and turkey, *m. longissimus dorsi* (LD) and *m. psoas major* (PM) from lamb and steak and fillet from ostrich. Data are expressed as means (S.D., $n=5$). Symbols for the significance of differences between muscle data for the same species: *** $P<0.001$; ** $P<0.01$; * $P<0.05$. ■ Thigh (chicken and turkey), breast (duck), PM (lamb). Oxidative muscles. □ Breast (chicken and turkey), thigh (duck), LD (lamb). Glycolytic muscles. ▨ Fillet (ostrich). ▧ Steak (ostrich).

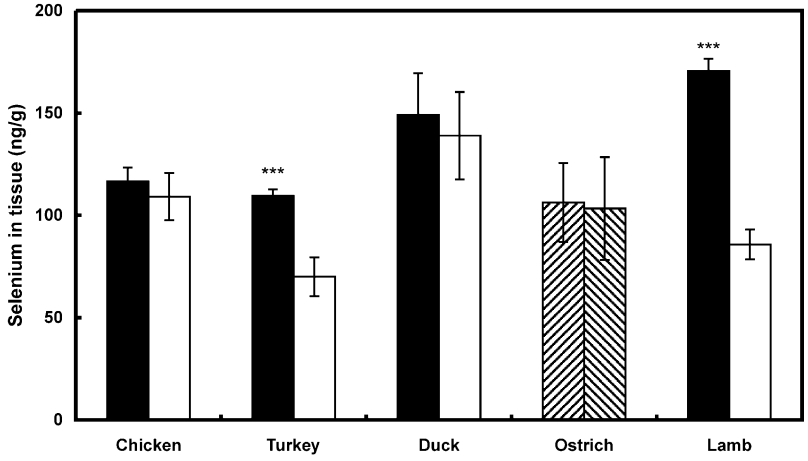

Fig. 2. Total selenium (ng/g) in breast and thigh muscles from chicken, duck and turkey, *m. longissimus dorsi* (LD) and *m. psoas major* (PM) from lamb and steak and fillet from ostrich. Data are expressed as means and (S.D., $n = 5$). Symbols for the significance of differences between muscle data for the same species: *** $P < 0.001$. ■ Thigh (chicken and turkey), breast (duck) and PM (lamb). Oxidative muscles. □ Breast (chicken and turkey), thigh (duck) and LD (lamb). Glycolytic muscles. ▨ Fillet (ostrich). ▧ Steak (ostrich).

Table 1
Content of soluble selenium in muscles from five species

	Breast	Thigh	LD	PM	Steak	Fillet	P^a
ng/g							
Chicken	70.9 (7.9)	88.6 (3.2)					0.008
Turkey	33.5 (4.7)	62.2 (1.7)					<0.001
Duck	109 (17.5)	87.6 (15.1)					0.004
Ostrich					68.8 (16.3)	72.8 (16.3)	0.77
Lamb			48.2 (3.0)	53.9 (3.6)			0.12
%							
Chicken	65.0 (1.9)	76.0 (4.0)					0.003
Turkey	47.9 (2.5)	56.8 (2.2)					0.008
Duck	73.4 (5.1)	63.0 (2.5)					0.004
Ostrich					67.8 (11.1)	68.7 (10.2)	0.66
Lamb			56.3 (2.2)	31.6 (1.4)			<0.001

The upper part of the table shows the content of soluble selenium expressed as ng/g in muscles. The lower part of the table shows the percentage (%) of soluble selenium out of total selenium in muscles. The data are expressed as means (S.D.) ($n = 5$).

[a] Significance of difference between the two muscles from each species (paired *t*-test).

3.4. Selenium content of feed

The content of selenium in the feed was analysed because it would be expected to be associated with the activity of GSHPx and selenium content in muscles. The feed given to the chickens, turkeys and ducks during various phases of breeding contained 0.34–0.62 mg selenium/kg (Table 2). The average selenium content in feeds given to the various birds was comparable, indicating that the variations in total and soluble selenium and GSHPx activity among these species were not due to the differences in selenium content of the feed.

Table 2
Selenium content in the feed given to chicken, turkey and duck

Feed sample	Selenium content (mg/kg fw)	Average (S.D.)
Chicken I	0.34	0.42
Chicken II	0.49	
Turkey I	0.46	0.49 (0.12)
Turkey II	0.38	
Turkey III	0.62	
Duck I	0.51	0.44
Duck II	0.38	

The numbers I–III indicate feeds given consecutively during animal growth.

3.5. Correlations between glutathione peroxidase activity and selenium

Since GSHPx is a selenoprotein it was of interest to study the associations between its activity and selenium content (total and soluble). A significant relationship between GSHPx activity and total selenium content in all muscles was found ($r = 0.63$, Fig. 3a). Although the number of samples for each muscle type and animal may be too low for the corresponding calculations within subgroups, such correlation coefficients were calculated (Table 3). A significant correlation between GSHPx activity and total selenium content was found only for duck thigh, but these variables also tended to correlate in ostrich fillet and turkey breast.

The same statistical analysis was made for the GSHPx activity and soluble selenium content (Fig. 3b). Data for these two variables in all muscles and species revealed a significant correlation ($r = 0.68$; $P < 0.01$), although the significance disappeared on exclusion of data from duck muscles ($r = 0.015$; $P = 0.93$). A significant relationship between the activity of GSHPx and soluble selenium within each species was found in both duck muscles and in chicken thigh (Table 3). As expected the total and soluble selenium contents were significantly correlated ($r = 0.60$; $P < 0.01$; Fig. 4). Using similar calculations within each species, significant correlations were obtained for breast muscle from chicken and turkey, both muscles from duck, and LD from lamb (Table 3).

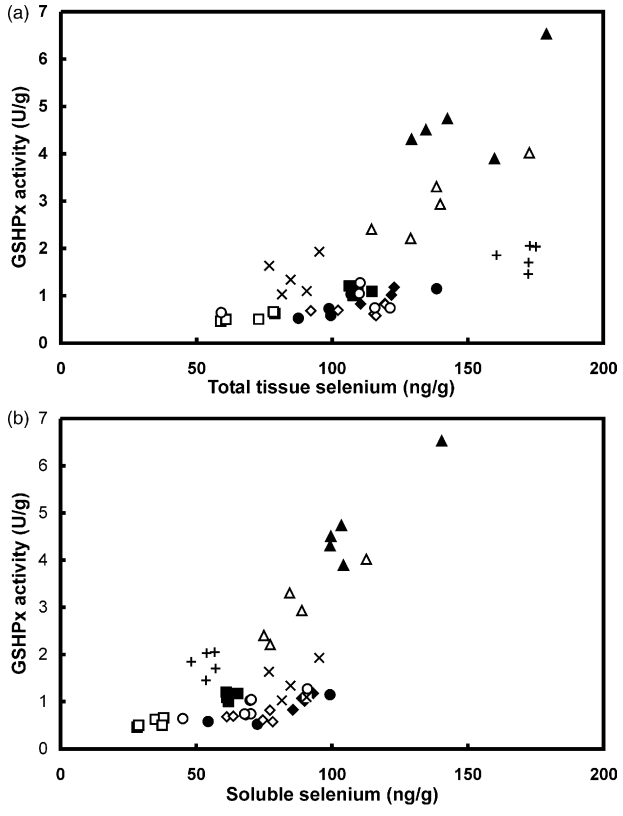

Fig. 3. (a) Scatterplot of GSHPx activity (U/g) versus total selenium (ng/g) in two muscles from each of five species. (◆) Chicken thigh; (▲) Duck breast; (+) Lamb PM; (•) Ostrich Fillet; (■) Turkey thigh (◇) Chicken breast; (△) Duck thigh; (x) Lamb LD; (○) Ostrich steak; (□) Turkey breast. (b) Scatterplot of GSHPx activity (U/g) versus soluble selenium (ng/g) in two muscles from each of five species. Symbols as in (a).

3.6. Ratio between glutathione peroxidase activity and selenium

To further study the association of GSHPx activity with selenium content, the ratios GSHPx/total selenium and GSHPx/soluble selenium were calculated (Fig. 5). These ratios were in a similar range for chicken, turkey and ostrich muscles. Higher ratios was observed for duck and lamb muscles, with an exception for lamb PM. If the specific activities of GSHPx in different tissues are similar, these findings would indicate that more of the total and soluble selenium is associated with GSHPx in duck and lamb muscles than in muscles from the other species.

4. Discussion

4.1. Glutathione peroxidase activity in muscles from different species

From the present study, it is apparent that the activity of GSHPx varies appreciably among muscles from different species. This extends previous similar findings made in muscle from experimental animals (Tappel, Chaudiere, & Tappel, 1982). The factors responsible for these differences in GSHPx activity in muscle are only partly known. In comparison with most of the data in previous studies, the GSHPx activity found by us in chicken and turkey muscles was somewhat higher (DeVore et al., 1983; Lee et al., 1996; Maraschiello, Sárraga & García Regueiro, 1999). The lowest GSHPx activity in the present paper, found in turkey breast muscle, was still higher than that previously found in pig *m. longissimus dorsi*, using the same method of analysis as in the present report (Daun et al., 2001). Lamb muscles had intermediate GSHPx activity, which was higher than that previously found in lamb leg muscle and quite similar to that found in bovine muscles (Daun et al., 2001; Moksnes & Norheim, 1983). Finally, our data on GSHPx activity in duck muscle were similar to previous findings (Xu & Diplock, 1983) whereas no previous data on GSHPx activity in ostrich have been found.

4.2. Distribution of selenium in muscle

Since the GSHPx activity was measured in the muscle supernatant it was interesting to measure the proportion

Table 3
Linear correlation coefficients between GSHPx activity vs. total selenium, GSHPx activity vs. soluble selenium and total selenium vs. soluble selenium in two muscles from each of five species

	GSHPx vs. total Se		GSHPx vs. soluble Se		Total Se vs. soluble Se	
	Breast/LD/steak *r*	Thigh/PM/fillet *r*	Breast/LD/steak *r*	Thigh/PM/fillet *r*	Breast/LD/steak *r*	Thigh/PM/fillet *r*
Chicken	0.04	0.28	−0.08	0.96**	0.97**	0.50
Turkey	0.87	−0.22	0.69	0.29	0.91*	−0.03
Duck	0.68	0.91*	0.94*	0.92*	0.88*	0.98**
Ostrich	0.38	0.87	0.85	0.72	0.74	0.80
Lamb	0.28	0.06	0.54	0.07	0.90*	0.84

* $P<0.05$; **$P<0.01$.

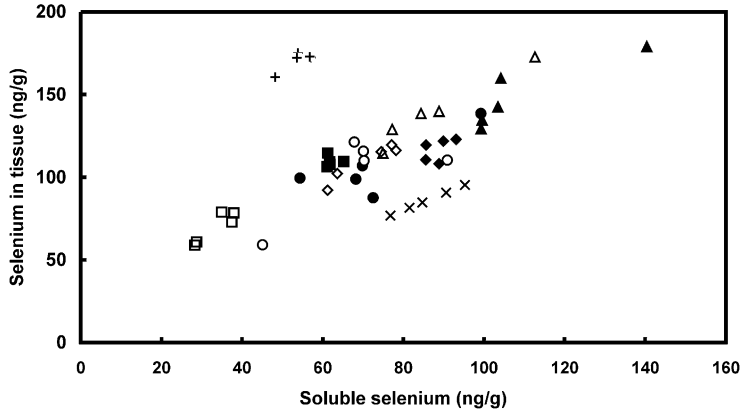

Fig. 4. Scatterplot of total selenium (ng/g) versus soluble selenium (ng/g) in two muscles from each of five species. Symbols as in Fig. 3a.

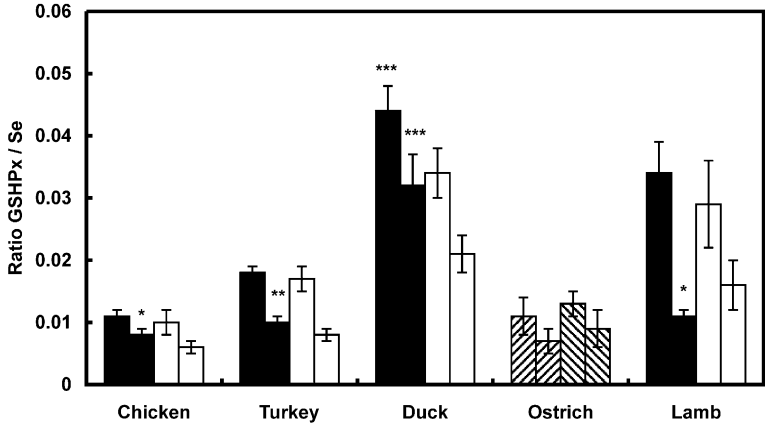

Fig. 5. Ratio between GSHPx activity (U/g) / soluble selenium (ng/g) (left column in each pair) and GSHPx activity (U/g)/total selenium (ng/g) (right column in each pair) in two muscles from each of five species. Symbols for the significance of differences between muscle data for the same species: *** $P<0.001$; ** $P<0.01$; *$P<0.05$. ■ Data on oxidative muscles. Thigh from chicken and turkey, breast from duck and PM from lamb. □ Data on glycolytic muscles. Breast from chicken, turkey, thigh from duck and LD from lamb. ▨ Fillet from ostrich. ▧ Steak from ostrich.

of soluble selenium in addition to total tissue selenium. Very few studies of the proportion of soluble selenium in muscle have been reported. The high percentage of soluble selenium in chicken thigh and duck breast was similar to that found previously in beef LD (72%), while most other muscles had values more comparable to that in beef PM (64%, Daun et al., 2001). The lower values found in turkey thigh and lamb LD were more similar to that previously found in pork LD (52%). Interestingly, lamb PM had a characteristic distribution of selenium with a high amount of total selenium but a low proportion of soluble selenium compared to all species (32%) while, conversely, lamb LD had a higher percentage of soluble selenium in combination with

significantly lower total selenium content. This shows that lamb PM contains a higher proportion of insoluble seleno compounds than lamb LD or muscles from the other species. The nature of these compounds is unknown. Another pattern was found in duck muscles which had a high selenium content, a high percentage of soluble selenium and a significantly higher GSHPx activity than lamb PM. This suggests that more of the soluble selenium in duck muscle is associated with GSHPx than is the case in lamb PM (assuming that the specific activities of the enzymes are similar). Thus, it seems that muscles have different distribution patterns of selenoproteins in several respects. This is in line with a previous comparison between beef muscle and pork (Daun et al., 2001), showing a lower ratio of GSHPx to total selenium and a lower percentage of soluble selenium in pork, indicating a higher proportion of non-GSHPx selenoproteins or other seleno compounds than in beef. Further speciation studies are necessary to evaluate the detailed distribution of seleno compounds in muscles from different species. In comparison, fish muscles contained soluble selenium in the range of 23–50% (Önning, 2000; Jia et al., 1996). The proportion of soluble muscle selenium in fish thus seems to be somewhat lower than that in most of the species investigated in the present study.

Although many new mammalian selenoproteins have recently been identified, only few of them have been studied in muscle. An exception in this respect is selenoprotein W, which is believed to play a protecting role against white muscle disease (Whanger, 2000). This selenoprotein is also, like GSHPx, affected by the amount of selenium in the feed and the highest level of selenoprotein W has been found in muscle and heart of selenium-supplemented lambs.

4.3. Selenium content of feed and muscle

Since the selenium content of muscle influences GSHPx activity, it was of interest to compare our selenium data with those in previous studies. The highest average total selenium content in the present study was found in the duck, followed by lamb > chicken > ostrich > turkey. Both lower and higher amounts of total selenium content in chicken white meat than in the present study have previously been reported (Higgs, Morris, & Levander, 1972; Díaz-Alarcón, Navarro-Alarcón, López-García de la Serrana, & López-Martínez, 1996). Our data on the selenium contents of chicken and turkey were lower than those obtained in Finland after the initiation of the use of selenate-supplemented fertilisers (Eurola, Ekholm, Ylinen, Koivistoinen, & Varo, 1991). Regarding the selenium content of duck meat, our results were comparable to those previously found (Dean & Combs, 1981). In the muscles from lamb we found a higher content than that obtained in lamb leg muscle (Moksnes & Norheim, 1983), but in LD it was somewhat lower than previous data for lamb chops (Higgs et al., 1972).

The content of selenium in muscle can be influenced by the amount and form of selenium in the soil and feed, and organic forms of selenium were found to have a higher bioavailability than other forms (Mahan & Parrett, 1996). The dietary need for selenium, to prevent deficiency diseases, is approximately the same for several animal species, ranging from 0.10 to 0.20 mg Se/kg feed (Combs & Combs, 1986). Since 1980, it has been permitted to supplement the feed of farm animals in Sweden with 0.1 mg selenium/kg. This amount was increased in 1993 to 0.5 mg total selenium/kg dry matter according to EU recommendations (Statens jordbruksverk, 1993).

Also the GSHPx activity in tissue and blood has been shown to be dependent on the form and amount of selenium in the feed (Cantor & Tarino, 1982; Moksnes & Norheim, 1983; Ortman, 1999; Xu & Diplock, 1983) and previous results indicate that supplementation with selenium can also increase GSHPx activity in muscle (DeVore et al., 1983). In the present study there was essentially no difference between the selenium amounts of the feed given to chicken (0.42 mg/kg), duck (0.44 mg/kg) and turkey (0.49 mg/kg), which means that the variation in the selenium concentration of the feed alone does not explain the higher GSHPx activity in duck muscle than muscles from other species.

4.4. Factors regulating the glutathione peroxidase activity in tissues

Much previous work has shown that GSHPx activity and selenium content are interrelated, especially for blood or serum. Only few such studies have been performed in muscle and very few have included the association between GSHPx activity and soluble selenium. In the present study, GSHPx activity was significantly correlated with both total and soluble selenium. The low number of animals from each species precluded a detailed assessment of the relationships for each species. In the previous study, such correlations were demonstrated in both beef muscle and pork (Daun et al., 2001). Also, DeVore and Greene (1982) have shown a significant correlation between GSHPx activity and total selenium content in *m. semitendinosus* from beef. These data show that, also in muscle, the selenium content is an important regulator of GSHPx activity.

Significantly higher ratios between GSHPx activity, and total or soluble selenium were observed for duck and lamb PM than in the other muscles studied. If the specific activities of GSHPx in different tissues are similar, this would mean that more of the total and soluble

selenium is associated with GSHPx in duck and lamb PM than in muscles from other species. An analogous finding was that pork LD contained a several-fold lower GSHPx activity than the two beef muscles (LD and PM) but a higher content of selenium (Daun et al., 2001).

The activity of GSHPx and the content of other selenoproteins in tissues are regulated by a number of other factors (Arthur, 2000; Köhrle et al., 2000). An early study suggested that the mRNA level and the efficiency of gene transcription determine the differences in GSHPx activity among species (Toyoda, Himeno, & Imura, 1989). Moreover, different GSHPx enzymes show specific tissue ranking (Brigelius-Flohé, 1999). Up-regulation of the mRNA by various mechanisms is one factor regulating the expression in different tissues (Flohé, Wingender, & Brigelius-Flohé, 1997), but other factors responsible for this ranking are not yet known. Since the GSHPx activity is also dependent on selenium in the feed, the mechanisms behind the effects of dietary selenium manipulation and the regulation of the expression of GSHPx genes have been studied (Brigelius-Flohé, 1999; Christensen, Cammack, & Wray, 1995; Toyoda et al., 1989), the results suggesting that the level of GSHPx mRNA is regulated by the dietary selenium at a post-transcriptional step (Toyoda, Himeno, & Imura, 1990).

4.5. Glutathione peroxidase activity and selenium in oxidative and glycolytic muscles

It is generally considered that oxidative muscles show higher activities of antioxidative enzymes than glycolytic muscles such as GSHPx (DeVore et al., 1983; Renerre, Dumont, & Gatellier, 1996). This was also found in the present study for most pairs of muscles and the findings are also in accordance with previous observations in turkey (Lee et al., 1996; Renerre et al., 1996) and chicken (DeVore et al., 1983). Furthermore, other antioxidative enzymes, superoxide dismutase and catalase, have also been shown to have a higher activity in oxidative than in glycolytic muscles (Renerre et al., 1996; Renerre, Poncet, Mercier, Gatellier, & Métro, 1999). The muscles with a high content of antioxidative enzymes would be expected to be more stable toward lipid oxidation but previous studies have instead shown that oxidative muscles are more prone to lipid oxidation than the glycolytic ones, mainly depending on their high content of fat and prooxidative forms of iron (Lee et al., 1996; Huang, Hultin, & Jafar, 1993; Kanner, Hazan, & Doll, 1988; Zenoble & Bowers, 1977). Maybe the deterioration in oxidative muscles would proceed even faster if they had a lower content of antioxidative enzymes. In several studies, supplementation of the feed with selenium was found to decrease lipid oxidation in chicken meat (Combs & Regenstein, 1980; DeVore et al., 1983) but not in beef (O'Grady et al., 2001). Further studies on the mechanisms of action of selenium compounds in this respect are needed.

The diversity in muscle GSHPx activity among and within species is probably due to different needs for protection by various kinds of antioxidants, GSHPx functioning together with other antioxidants and/or antioxidative enzymes, acting in a complementary manner. Selenium ingested from the feed is used for the synthesis of different selenoproteins, which is regulated in a selenium- and tissue-dependent hierarchy. Further studies on the role of newly detected selenoproteins for meat quality are thus required.

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