ABSTRACT

The objectives of this study were to determine oxygen consumption by portal-drained viscera and liver in lactating ewes and to determine the relationship between this consumption and milk production. Nine multiparous ewes were individually penned and fed for ad libitum intake a diet based on alfalfa hay. Catheters were surgically placed in the portal vein, a branch of the hepatic vein, a mesenteric vein, and the abdominal aorta. Oxygen consumption by portal-drained viscera and liver was subsequently measured at 1, 3, 6, and 10 wk after parturition. The percentages of fat, protein, and SNF in milk decreased as milk production increased; however, yields of fat, protein, and SNF increased as milk production increased. Increased oxygen consumption by portal-drained viscera and liver was positively correlated with increased milk energy yield. These results indicated that the efficiency of milk energy secretion relative to energy expenditure by these tissues increases as milk production increases.

(Key words: sheep, lactation, metabolism, liver)

Abbreviation key: p-AH = p-aminohippuric acid,
PDV = portal-drained viscera.

INTRODUCTION

The genetic capacity of the female and the metabolites available for milk biosynthesis both contribute to milk production. Metabolites for milk biosynthesis may be derived from increased dietary intake or from mobilization of maternal tissues (30). Portal-drained viscera (PDV) and liver are principle support tissues that provide the mammary gland with metabolites. Oxygen consumption by PDV has been shown to be correlated with feed intake (5, 11, 12, 21). Increases in feed intake to support increased milk production would be expected to be positively correlated with an increase in the oxygen consumption of PDV. The liver directly supports milk production by being a net producer of glucose and acetate (13) and indirectly supports lactation through synthesis of urea, ketones, and triacylglycerides. The liver supports milk synthesis regardless of whether metabolites originate from the diet or from maternal tissues, suggesting that metabolic activity of the liver increases as milk production increases. Previous studies in the cow have identified PDV and liver as primary contributors to total oxygen consumption (16, 24); however, the effect of milk production on aerobic metabolism by these tissues has not been addressed. The objective of this study was to determine oxygen consumption by PDV and liver in lactating ewes and to determine the relationship between milk production and oxygen consumption by these tissues.

MATERIALS AND METHODS

Management of Ewes

Nine polled Dorset ewes that had previously been used in a pregnancy study (11) were housed in individual pens (2.88 m²). To ensure a range in milk production, dry ewes (n = 2) and ewes nursing one (n = 3) or two (n = 4) lambs were used. Room temperature was kept at 20°C, and photoperiod was 12 h of light followed by 12 h of darkness. Ewes weighed 84.0 ± 2.1 kg and were fed a pelleted diet (57% dehydrated alfalfa, 28% corn cobs, and 15% corn) for ad libitum intake. The digestible energy content of the diet was 2.09 Mcal/kg (as-fed basis) (11). Ewes were fed daily at 1400 h, and orts from the previous day were determined at feeding. Water was provided for ad libitum intake. Catheters were surgically placed in the portal vein, a branch of the hepatic vein, a mesenteric vein, and in the abdominal aorta as described by Ferrell et al. (9). Sample collection began 200 d after surgery. Ewes had been acclimated to the animal facilities and to the collection procedure over the 6-mo period before sample collection. Experimental procedures were conducted in accordance with the
animal care guidelines of the Roman L. Hruska US Meat Animal Research Center (Clay Center, NE) and the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (14).

Sample Protocol

The week after parturition, sample collection began. On the day of sampling, the mammary gland was completely milked out by hand, and ewes were transferred to a metabolism crate at 0730 h. Lambs were allowed physical contact with the ewe during the sample collection but were denied access to the mammary gland. A priming dose (15 ml) of p-aminohippuric acid (p-AH; 0.15 M) was administered via the mesenteric vein followed by a constant infusion of p-AH at 0.8 ml/min. Sixty minutes following the priming dose, blood samples (10 ml) were drawn into heparinized syringes from the aortic, portal venous, and hepatic venous catheters. Samples were collected at 40-min intervals for a total of seven sets (aortic, portal venous, and hepatic venous) of samples. An additional 1.0 ml of blood was drawn into heparinized syringes and analyzed immediately to determine hemoglobin and the percentage of oxygen saturation of hemoglobin (Hemoximeter®, model OSM-2; Radiometer America Inc., Westlake, OH). After blood samples were collected, 6-h milk production was determined by completely milking the right half of the mammary gland. Simultaneously, lambs were allowed to suckle the left half of the mammary gland. Milk production was calculated as milk weight multiplied by 2. Additional samples were collected as indicated previously at 3, 6, and 10 wk of lactation.

Fresh blood samples were diluted 1:4 (vol/vol) with deionized water to analyze p-AH. Blood samples were analyzed for p-AH by automated procedures (no. 216-72T; Technicon Industrial Systems, Ardlie, NY). Oxygen concentrations were calculated as described by Burrin et al. (5).

Blood flow was calculated using an indicator dilution technique as described previously (17). Net fluxes of metabolites were calculated by multiplying blood flow by the concentration difference in the vessels (17). Daily observations were the means of the seven replicate samples.

Milk samples were weighed and analyzed for fat, protein, lactose, and SNF with an infrared spectrophotometer (model B-2000; Bentley Instruments, Chaska, MN). Milk samples were freeze-dried, and energy content was determined (1).

Quadratic regressions were initially tested, and a step-down procedure was used to remove independent variables that did not contribute to the regression model. Regression analyses were conducted using the GLM procedure of SAS (25). Mean separations were analyzed as a split plot using the GLM procedure of SAS (25). Differences between means were tested with a linear model that included ewe, treatment, and period as discrete effects. The model consisted of treatment, ewe nested within treatment, period, and the interaction of treatment and period. Treatment means were tested, and ewe nested within treatment was the source of error. Means associated with milk production were tested with the same model after the nonlactating ewes were removed from the data file. For the sake of discussion, differences were determined at $P < 0.05$.

RESULTS

The BW of the ewes was not affected by litter size ($P = 1.00$) or by collection period ($P = 0.29$). There was an interaction between litter size and period for the feed intake of ewes housed individually in pens ($P = 0.0001$). The feed intakes of nonpregnant ewes were 2037, 1873, 1675, and $903 \pm 238$ g/d ($X \pm SE$) at 1, 3, 6, and 10 wk after parturition, respectively. While ewes were housed in individual pens, those nursing single lambs had feed intakes of 2295, 3415, 3418, and $3840 \pm 194$ g/d at 1, 3, 6, and 10 wk after parturition, respectively. Also, while ewes were housed in individual pens, those nursing twin lambs had feed intakes of 2504, 3830, 4234, and $4547 \pm 168$ g/d at 1, 3, 6, and 10 wk after parturition, respectively. Feed intakes during wk 1 and 3 were representative of feed intakes by the ewe alone, and feed intakes during wk 6 and 10 are cumulative feed intakes for the ewe and her lambs. In early lactation (wk 1 and 3), oxygen consumption by PDV and liver increased as digestible energy intake increased (Table 1). Similarly, milk production was positively related to digestible energy intake (Table 1).

Milk

The concentration of fat, protein, SNF, and energy in milk decreased as milk production increased; however, the total yields of fat, protein, SNF, and energy increased as milk production increased (Table 2). Percentage of lactose was not affected by level of milk production ($5.99 \pm 0.21; P = 0.35$), but lactose yield increased as milk production increased (Table 2).

Milk production [$f(x)$; grams per hour] by ewes nursing single lambs did not change with stage of lactation ($x$; days). The regression was $f(x) = 0.02(x) + 38.5$; $r^2 = 0.002; P = 0.89$. A curvilinear
TABLE 1. Regression of oxygen consumption by splanchnic tissues and milk production \( f(x) \) on digestible energy intake in early lactation.\(^1\)

<table>
<thead>
<tr>
<th>Regression coefficients</th>
<th>b(_2)</th>
<th>SE</th>
<th>b(_1)</th>
<th>SE</th>
<th>b(_0)</th>
<th>SE</th>
<th>R(^2)</th>
<th>P &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>PDV(^3) ( O_2 ), mmol/h</td>
<td>...</td>
<td>...</td>
<td>0.020</td>
<td>0.006</td>
<td>199.5</td>
<td>36.4</td>
<td>0.38</td>
<td>0.007</td>
</tr>
<tr>
<td>Hepatic ( O_2 ), mmol/h</td>
<td>...</td>
<td>...</td>
<td>0.031</td>
<td>0.008</td>
<td>154.1</td>
<td>43.8</td>
<td>0.50</td>
<td>0.001</td>
</tr>
<tr>
<td>Milk, g/h</td>
<td>-0.0000038</td>
<td>0.0000018</td>
<td>0.057</td>
<td>0.022</td>
<td>-155.2</td>
<td>64.9</td>
<td>0.62</td>
<td>0.0007</td>
</tr>
<tr>
<td>Milk, kcal/h</td>
<td>-0.0000044</td>
<td>0.0000017</td>
<td>0.063</td>
<td>0.021</td>
<td>-168.6</td>
<td>61.6</td>
<td>0.58</td>
<td>0.001</td>
</tr>
</tbody>
</table>

\(^1\)Data are from wk 1 and 3 after parturition and include two measurements on each of seven lactating ewes and each of two nonlactating ewes.

\(^2\)\( f(x) = b_2(x)^2 + b_1(x) + b_0 \), where \( x = \) kilocalories of digestible energy per day.

\(^3\)Portal-drained viscera.

The energy content of milk was linearly related to the fat and SNF contents of milk (Table 3). The precision of the estimate of energy content did not change when the content of protein and lactose was substituted for SNF. The precision of the estimate remained the same when lactose content was removed; however, the precision decreased when only fat content was used to predict energy content.

**Blood Flow and Oxygen Consumption**

Blood flow in the hepatic artery, the portal vein, and the hepatic vein increased as milk production increased (Table 4). Differences in arterial-venous and portal-hepatic venous oxygen concentrations increased as milk production increased. Oxygen consumption by PDV (millimoles per hour) was linearly related to portal venous blood flow (liters per hour): \( f(x) = 1.88(x) - 38.61; r^2 = 0.71 \). Oxygen consumption by the liver was linearly related to hepatic venous blood flow: \( f(x) = 1.60(x) - 52.63; r^2 = 0.67 \). Oxygen consumption by PDV and liver was linearly related to milk production (Figure 1). Oxygen consumption by the combined splanchnic tissues (PDV + liver; millimoles per hour) was linearly related to milk production (grams per hour): \( f(x) = 4.77(x) + 409.00; r^2 = 0.67 \).

**DISCUSSION**

In the current study, a wide range in milk production was achieved by sampling ewes with different litter sizes at different stages of lactation. Previous studies have demonstrated that milk production varies with litter size and stage of lactation (6, 23, 28). Milking frequency has also been demonstrated to

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**TABLE 2. Regression of milk composition and milk component yield \( f(x) \) on milk production.\(^1\)**

<table>
<thead>
<tr>
<th>Regression coefficients</th>
<th>b(_1)</th>
<th>SE</th>
<th>b(_0)</th>
<th>SE</th>
<th>( r^2 )</th>
<th>P &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Composition</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Energy, cal/g</td>
<td>-3.80</td>
<td>1.39</td>
<td>1137.16</td>
<td>67.16</td>
<td>0.22</td>
<td>0.01</td>
</tr>
<tr>
<td>Fat, %</td>
<td>-0.040</td>
<td>0.014</td>
<td>7.380</td>
<td>0.688</td>
<td>0.23</td>
<td>0.01</td>
</tr>
<tr>
<td>Protein, %</td>
<td>-0.016</td>
<td>0.006</td>
<td>5.861</td>
<td>0.279</td>
<td>0.23</td>
<td>0.01</td>
</tr>
<tr>
<td>SNF, %</td>
<td>-0.039</td>
<td>0.018</td>
<td>13.939</td>
<td>0.869</td>
<td>0.15</td>
<td>0.04</td>
</tr>
<tr>
<td>Lactose, %</td>
<td>-0.013</td>
<td>0.013</td>
<td>6.572</td>
<td>0.649</td>
<td>0.03</td>
<td>0.35</td>
</tr>
<tr>
<td>Yield</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Energy, kcal/h</td>
<td>0.773</td>
<td>0.060</td>
<td>7.73</td>
<td>2.89</td>
<td>0.87</td>
<td>0.0001</td>
</tr>
<tr>
<td>Fat, g/h</td>
<td>0.034</td>
<td>0.007</td>
<td>0.908</td>
<td>0.317</td>
<td>0.50</td>
<td>0.0001</td>
</tr>
<tr>
<td>Protein, g/h</td>
<td>0.045</td>
<td>0.003</td>
<td>0.256</td>
<td>0.138</td>
<td>0.90</td>
<td>0.0001</td>
</tr>
<tr>
<td>SNF, g/h</td>
<td>0.104</td>
<td>0.007</td>
<td>0.703</td>
<td>0.346</td>
<td>0.89</td>
<td>0.0001</td>
</tr>
<tr>
<td>Lactose, g/h</td>
<td>0.053</td>
<td>0.006</td>
<td>0.287</td>
<td>0.270</td>
<td>0.78</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

\(^1\)Data are from four measurements on each of seven ewes.

\(^2\)\( f(x) = b_1(x) + b_0 \), where \( x = \) grams of milk per hour.
TABLE 3. Regressions for the estimation of energy in the milk of ewes based on composition. 1

<table>
<thead>
<tr>
<th>Regression coefficients</th>
<th>( b_4 )</th>
<th>SE</th>
<th>( b_3 )</th>
<th>SE</th>
<th>( b_2 )</th>
<th>SE</th>
<th>( b_1 )</th>
<th>SE</th>
<th>( b_0 )</th>
<th>SE</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>86.2</td>
<td>8.7</td>
<td>\ldots</td>
<td>\ldots</td>
<td>\ldots</td>
<td>12.7</td>
<td>7.2</td>
<td>329.4</td>
<td>103.2</td>
<td>0.80</td>
<td></td>
<td></td>
</tr>
<tr>
<td>87.6</td>
<td>8.9</td>
<td>37.3</td>
<td>22.5</td>
<td>\ldots</td>
<td>3.0</td>
<td>10.8</td>
<td>\ldots</td>
<td>\ldots</td>
<td>287.4</td>
<td>127.0</td>
<td>0.80</td>
</tr>
<tr>
<td>87.6</td>
<td>8.8</td>
<td>38.7</td>
<td>21.6</td>
<td>\ldots</td>
<td>\ldots</td>
<td>\ldots</td>
<td>287.4</td>
<td>127.0</td>
<td>0.80</td>
<td></td>
<td></td>
</tr>
<tr>
<td>85.5</td>
<td>9.0</td>
<td>\ldots</td>
<td>\ldots</td>
<td>\ldots</td>
<td>\ldots</td>
<td>\ldots</td>
<td>487.7</td>
<td>51.7</td>
<td>0.77</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1Data are from four measurements on each of seven ewes. Milk energy (calories per gram) = \( b_4 \times \) fat (percentage) + \( b_3 \times \) protein (percentage) + \( b_2 \times \) lactose (percentage) + \( b_1 \times \) SNF (percentage) + \( b_0 \).

TABLE 4. Regression of blood flow and oxygen concentration \( f(x) \) on milk production. 1

<table>
<thead>
<tr>
<th>Regression coefficients</th>
<th>( f(x) )</th>
<th>( b_1 )</th>
<th>SE</th>
<th>( b_0 )</th>
<th>SE</th>
<th>( R^2 )</th>
<th>( P &gt; F )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blood flow, L/h</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hepatic arterial</td>
<td>0.29</td>
<td>0.13</td>
<td>29.47</td>
<td>5.34</td>
<td>0.13</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>Portal venous</td>
<td>0.78</td>
<td>0.17</td>
<td>146.41</td>
<td>7.34</td>
<td>0.37</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>Hepatic venous</td>
<td>1.07</td>
<td>0.23</td>
<td>175.89</td>
<td>9.82</td>
<td>0.39</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>Oxygen concentration, mmol/L</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arterial</td>
<td>0.009</td>
<td>0.003</td>
<td>6.421</td>
<td>0.142</td>
<td>0.18</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>Arterial-portal</td>
<td>0.007</td>
<td>0.001</td>
<td>1.420</td>
<td>0.053</td>
<td>0.46</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>Arterial-hepatic</td>
<td>0.010</td>
<td>0.083</td>
<td>2.361</td>
<td>0.083</td>
<td>0.42</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>Portal-hepatic</td>
<td>0.003</td>
<td>0.001</td>
<td>0.941</td>
<td>0.051</td>
<td>0.16</td>
<td>0.01</td>
<td></td>
</tr>
</tbody>
</table>

1Data are from four measurements on each of nine ewes.

\( f(x) = b_1(x) + b_0 \), where \( x \) = grams of milk per hour.

Influence milk production (19). The 6-h milking period in the current study did not reflect the maximum synthetic capacity of the mammary gland, but did reflect the amount of milk that was synthesized while the oxygen consumption of PDV and liver was measured. Peak lactation occurred around 3 wk after parturition, which is consistent with the findings of Corbett (6). As in this study, Corbett (6) found that the percentages of milk fat and milk protein decreased as milk production increased, and yields of milk fat and milk protein increased as milk production increased. Lactose concentration was not related to milk production; therefore, lactose yield increased as milk production increased. When a multiregression analysis was used to predict energy content based on milk composition, the addition of lactose to the equation did not improve the estimate. These relationships are consistent with those found for dairy ewes (4). Corbett et al. (7) demonstrated that, in the 6th wk of lactation, intake of metabolizable energy by ewes increased 73% relative to that by nonlactating ewes. Those researchers (7) also found that the metabolizable energy that is required for maintenance increased (37%) from 134 kcal/kg^{0.75} to 178 kcal/kg^{0.75}. Smith and Baldwin (26) estimated that the increase in heat production by the mammary gland accounted for 17% of the increase in energy expenditures that were associated with milk production by the cow. In the same study (26), those researchers estimated that heat production in the gastrointestinal tract increased 28% and that heat production by the liver increased 25% during lactation. These estimates are consistent with the observed proportions of total oxygen consumption by the cow for the PDV (0.20) and liver (0.25) as measured by Reynolds et al. (24). The estimates of Smith and Baldwin (26) are based partially on changes in organ weight between lactating and nonlactating cows. Increases in the weight of the abomasum, intestine, and liver have been demonstrated in lactating compared with nonlactating ewes (8).

Based on the regressions in Figure 1, a ewe with a milk production of 76 g/h would have an 83% increase in aerobic metabolism of the PDV and a 95% increase in aerobic metabolism of the liver compared with a nonlactating ewe. In the studies of Corbett et al. (7), lactating ewes had a daily heat production of 4019 kcal/d, and milk energy yield was 1603 kcal/d. Based on the regression equations from this study, we estimated a milk production of 76 g/h, which corresponds to oxygen consumption by the PDV of 380 mmol/h and oxygen consumption by the liver of 392 mmol/h. If it is assumed that 110 kcal/mol of O_2 are produced...
then the PDV and liver each represent approximately 25% of total heat production. These values are similar to those observed for lactating cows (24) in which PDV accounted for 20.4% and liver accounted for 25.3% of the total oxygen consumption of the cow.

As milk production increased, PDV and hepatic energy expenditure increased (Figure 2). If splanchnic energy expenditure represents 50% of the total energy expenditure of the ewe, the increase in 

![Graph](image)

Figure 1. Relationship between oxygen consumption of portal-drained viscera (PDV) and milk production in the ewe; slope = 2.26 ± 0.29, intercept = 207.8 ± 12.3, and \( r^2 = 0.64 \) (a). Relationship between hepatic oxygen consumption and milk production in the ewe; slope = 2.51 ± 0.38, intercept = 201.2 ± 16.4, and \( r^2 = 0.56 \) (b). A different ewe is represented by each symbol.

splanchnic energy expenditure as milk production increases suggest that total heat production by the ewe increases as milk production increases. An increase in total heat production by the animal as milk energy secretion increases has been observed for cows (10, 22). As milk production increases, the rate of increase in milk energy secretion relative to the rate of increase in expenditure of splanchnic tissue energy increases (Figure 2). These differences suggest that the efficiency of milk production with respect to expenditure of splanchnic energy increases as milk production increases. Results for the cows (10, 22) support those findings; the ratio of milk energy to total heat production of the cow increased as the yield of milk energy increased.

Increases in the metabolic rate of PDV and liver as milk production increased were probably due to increased demand on these tissues to support lactation. Ad libitum feed intake of lactating ewes during early lactation increased above that of nonlactating ewes. Other studies have reported a positive relationship between level of milk production in ewes fed a restricted diet (28) and ewes that had ad libitum access to feed (23). Previous studies with feed-restricted sheep and sheep fed ad libitum consumption have demonstrated that oxygen consumption by PDV is positively correlated with feed intake (5, 11, 12, 21). Weekes (29) reported that enzymatic activity per unit of tissue involved with the conversion of propionate to lactate and pyruvate in ruminal mucosal cells did not change during lactation; however, because of the increase in tissue weight, total activity increased. For both lactating ewes and cows, tissues that contribute to energy expenditure by PDV increase in weight compared with those same tissues in nonlactating ewes and cows (8, 26).

Metabolites for milk biosynthesis may be derived from increased dietary intake or from mobilization of maternal tissues (30). One adaptation to support lactation is an increase in feed intake. Similar to oxygen consumption by the PDV, the oxygen consumption by the liver also has been shown to be correlated with feed intake (5, 11, 12, 21). The increase in oxygen consumption by the liver represents the increased demand on the tissue to support the mammary gland. Using a model of mammary gland metabolism in the lactating cow, Hanigan and Baldwin (15) estimated that 27% of the total energy uptake by the gland was as glucose and 14% was as acetate, both of which are products of liver metabolism in the lactating cow (13). In lactating ewes, plasma glucose entry tends to be higher in ewes nursing twins than in ewes nursing single lambs,
tire, these data suggest that neither apparent maintenance nor the partial efficiency of lactation remains constant for different levels of milk production.

**CONCLUSIONS**

In the lactating ewe, aerobic metabolism of the PDV and liver contributes to a large proportion of the total oxygen consumption by the ewe. Oxygen consumption by the PDV and liver increased as milk production increased, and the efficiency of milk energy secretion relative to energy expenditure by these tissues increased as milk production increased. Because the contribution of the PDV and liver represents a high proportion of total energy expenditure, these data suggest that neither apparent maintenance nor the partial efficiency of lactation remains constant for different levels of milk production.

**ACKNOWLEDGMENT**

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