ABSTRACT: Thirty-two crossbred lambs (BW = 31.2 ± 4.7 kg; 16 females, 16 males) housed in individual pens were used to investigate the relationship between nutrient supply and taste preferences in ruminants. Experiment 1 determined whether an imbalanced CP supply would alter preferences for feeds containing flavors designed to elicit either umami (U) or a mixture (1/3:1/3:1/3) of umami, sweet, and bitter (M) tastes. Lambs were randomly allocated to either a low (LP; 10.9% CP) or a high (HP; 20.4% CP) CP diet for 21 d. Afterward, lambs were presented during 21 d with a choice of the same LP or HP diet unflavored (LPC or HPC, respectively) or flavored (0.1% as fed) with U (LPU or HPU, respectively) or M (LPM or HPM). Experiment 2 determined the influence of CP status on preference for dietary CP, bitter taste, and sweet taste elicited by sucrose or a noncaloric sweetener. In test 1, sixteen lambs previously fed LP or HP for 42 d in Exp. 1 could choose between the HP and LP diets. In test 2, the remaining 16 lambs from Exp. 1 were offered a choice between unflavored LP or HP diets or the same diets flavored (0.066% as fed) with a bitter flavor. In test 3, the 16 lambs from test 1 were offered a choice between an unflavored diet (LP or HP) and the same diet flavored with sucrose (0.2%) or a noncaloric sweetener (0.066%). In Exp. 1, when offered a choice, all lambs showed a preference (P < 0.05) for the unflavored diet except for LP lambs, who clearly preferred (P < 0.05) LPU (72% of total DMI) over LPC. However, preference for LPU progressively decreased (P < 0.05) as time of exposure to the choice increased. In Exp. 2 (test 1), lambs previously fed LP progressively increased (P < 0.05) total DMI when presented with LP and HP, whereas consumption was constant for lambs previously fed HP and offered a choice of LP and HP diets. At the onset of test 2, lambs fed LP progressively reduced (P < 0.05) preference for the bitter flavor from 53 to 34%. In test 3, lambs previously fed LP diets consumed less (P < 0.05) sweetener- than sucrose-supplemented diet, whereas lambs previously offered HP diets consumed more sweetener- than sucrose-supplemented diet. In summary, protein-restricted lambs were able to differentiate and increase consumption of U-flavored feeds. However, this increase disappeared over time. These results indicate that lambs are able to sense dietary CP content and modulate short-term consumption of flavored feeds based on their nutrient requirements.

Key words: bitter, eating pattern, flavor, sweet, umami

©2012 American Society of Animal Science. All rights reserved.

INTRODUCTION

Ruminants and other mammals are thought to regulate feed intake based on nutritional needs (Forbes, 1977b), physical limitations (Forbes, 1977a), hedonics and taste (Gallouin and Le Magnen, 1987), and postigestive feedback mechanisms (Provenza 1995; Provenza and Villalba, 2006). A fundamental question that remains to be answered is the extent to which palatability-enhancing properties of flavors are learned or affected by physiological state of the animal. For instance, the taste elicited by the sodium salt of the AA l-glutamate (umami) has been long recognized as
different from any of the basic tastes (sweet, sour, salty, bitter), and it has been proposed to help animals detect sources of protein in a manner analogous to that for sweet taste, which may signal calories from carbohydrates (Beauchamp, 2009). Palatability studies in different animals and ages have confirmed that the addition of umami to feeds increases feed preference (Tedó, 2009). However, there is little evidence that a protein deficiency may enhance consumption of umami-tasting feeds (Beauchamp, 2009).

The first 2 objectives of this study were to determine whether growing animals would be able to regulate intake based on the dietary CP content, and whether a shortage of protein supply would enhance preference for an umami-flavored feed.

It has been argued that perception and preference for foods through umami taste may be enhanced by other taste qualities. For instance, bitter-tasting ligands can bind to umami receptors, rather than bitter receptors, and elicit the bitter sensation through cross-stimulation (Temussi, 2009). Thus, the third objective of this study was to explore whether the physiological need for protein influences preferences not only for umami, but also for other flavors that are associated (or perceived by the animal) with the presence of calories (sweet) or plant secondary compounds (bitter) that could exert a cross-stimulation of umami receptors.

**MATERIALS AND METHODS**

The study was conducted according to procedures approved by the Utah State University Institutional Animal Care and Use Committee at the Green Canyon Ecology Center of Utah State University in Logan.

**Exp. 1: Interaction Between Protein Supply and Feed Flavor**

This experiment aimed at determining whether an imbalanced protein supply would alter preferences for feeds flavored with umami or a mixture of umami, bitter, and sweet flavors. Thirty-two Finn-Columbia-Polypay-Suffolk crossbred lambs (2 mo of age; 16 females, 16 males) with an average initial BW of 31.2 ± 4.7 kg were distributed in individual pens (0.4 × 3.6 m). Lambs were able to establish visual and physical contact through the pen walls. Throughout the study, lambs had free access to fresh water and salt blocks (containing calcium, phosphorous, and trace minerals). Animals were randomly allocated to either a low (LP; 10.9% CP; n = 16) or a high CP (HP; 20.4% CP; n = 16) diet for 21 d. Lambs were fed ad libitum once daily at 0800 h. After 21 d of adaptation to the diets, lambs in the LP group were presented for an additional 21 d with a choice consisting of 2 buckets containing the respective unflavored (control) diets (LPC or HPC, respectively) or the same diets flavored (0.1% as fed) either with umami (LPU or HPU, respectively) or a mixture (1/3:1/3:1/3) of umami (Luctarom ref-5433), bitter (Luctarom ref-5432), and sweet (Luctarom ref-5431) flavors (LPM or HPM, respectively). Thus, 4 groups of 8 lambs were presented with a choice between LPC and LPU, LPC and LPM, HPC and HPU, and HPC and HPM. Flavors were developed and supplied by Lucta S.A. (Montornés del Vallés, Spain). Ingredient and nutrient composition of the experimental diets is depicted in Table 1.

Feed refusals and intake were recorded on a daily basis. Lambs were weighed on 2 consecutive days before feeding time at the beginning of the study, and at the beginning (after 21 d of exposure to LP and HP diets) and at the end (after 21 d of exposure to double choices) of the experimental period. In addition, on d 1, 4, 11, and 18 of the experimental period, lambs were fed at 0800 h, and intake was measured every 60 min for 9 h to determine eating pattern and rate.

After 2 wk of being exposed to LP and HP diets, blood samples were collected from all lambs by puncture of a jugular vein −30 and 60 min relative to feeding to determine blood urea N (BUN) concentration as an indicator of the protein status of the animal (Hoffman et al., 2007). Samples were collected in vials (10 mL) without anticoagulant additives (BD Vacutainer, Franklin Lakes, NJ). Blood samples were kept in ice for about 30 min and then centrifuged at 3,000 × g for 20 min at 4°C to harvest serum and subsequently stored at −30°C until analyses. Blood urea N analyses were performed at the local hospital (Logan Regional Hospital) on a Vitro 950 Clinical Analyzer (Ortho Clinical Diagnostics, Rochester, NY) with an intraassay CV of 1.6%. The standard curves were linear within the range of 2 to 120 mg/dL, and precision limits were ≤0.61 mg/dL.

**Exp. 2: Diet Selection Based on Nutrient and Flavor Preferences**

Immediately after completing Exp. 1, three different concatenated 7-d tests (with no adaptation period between them) were performed. In the first test, lambs exposed in Exp. 1 to the LPU and HPU diets (n = 16) were offered a choice between the unflavored HP and LP diets to assess whether previous dietary CP concentration would influence subsequent selection of LP and HP diets and to determine the final CP intake they would reach within 7 d. For this reason, no adaptation period was allowed between Exp. 1 and 2. In the second test, lambs offered the LPM and HPM diets (n = 16) in Exp. 1 were exposed to a choice of their respective unflavored LP or HP diets and the same LP or HP diets flavored (0.066% as fed basis) with the bitter flavor used in Exp. 1 to assess the interaction between CP supply and preference for the bitter taste. In the third test, the 16 lambs that participated in test 1 were randomly divided into 2 groups and offered a choice between the unflavored LP (n = 8) or HP (n = 8) diet and the same diet flavored with sucrose (0.2%, as-fed...
basis) or a noncaloric sweet flavor (0.066%, as-fed basis) used in Exp. 1 to evaluate whether lambs would show a preference for sweet supplied by sucrose or to a noncaloric sweetener depending on the CP level of the ration.

As described in Exp. 1, feed intake was monitored daily and the eating pattern was assessed on d 7 of each test during the 9 h after feed offer, and eating rate was estimated by determining the feed consumed every hour at each sampling time. In this case, however, animal performance was not monitored due to the short duration of each test.

Calculations and Statistical Analyses

Data from the 2 experiments were processed and analyzed in a similar manner. Individual BW of 2 consecutive days were averaged and used as a single measure of BW at each time point (beginning of study, and beginning and end of experimental period). All data analyses were conducted using SAS (SAS Inst. Inc. Cary, NC).

Feed intake and growth performance (BW and ADG) were analyzed using a mixed-effects model that accounted for the random effect of animal within treatment, and the fixed effects of treatment, time of measurement, and their interaction. Time entered the model as a repeated measure. The variance-covariance structure used was the autoregressive order 1 (which yielded the smallest Bayesian information criterion). Data pertaining to eating pattern and concentration of blood metabolites were averaged across days within animal and then analyzed as double repeated measures (time of the day and day of sampling). Time of the day or hour was modeled with an unstructured variance-covariance structure and sampling day as autoregressive order 1. When the interaction between day and hour was significant, data were analyzed separately by sampling day to ease interpretation.

RESULTS AND DISCUSSION

Exp. 1: Interaction Between Protein Supply and Feed Flavor

Impact of Protein Supply on Intake and BUN. During the first 21 d of study (when only LP and HP diets were offered), average intake was reduced (P < 0.001) in lambs consuming LP (947 ± 51.6 g/d) compared with HP (1,166 ± 51.7 g/d), and there was a tendency (P = 0.09) for this difference to increase over time (Figure 1). It has been previously reported that when protein is limiting, voluntary DMI may decrease dramatically because of metabolic limitations to processing energy (Fisher, 2002). Similarly to the current study, Tolkamp et al. (1998) reported a reduced feed consumption in dairy cows consuming a low-CP diet compared with those offered a high-CP ration.

Analyses of blood samples obtained 30 min before feeding 14 d from the onset of the experiment revealed a decreased (P < 0.001) BUN concentration in LP (7.63 ± 1.07 mg/dL) compared with HP (18.81 ± 1.07 mg/dL) lambs, and there was a tendency (P = 0.09) for this difference to increase over time (Figure 1). It has been previously reported that when protein is limiting, voluntary DMI may decrease dramatically because of metabolic limitations to processing energy (Fisher, 2002). Similarly to the current study, Tolkamp et al. (1998) reported a reduced feed consumption in dairy cows consuming a low-CP diet compared with those offered a high-CP ration.

Analyses of blood samples obtained 30 min before feeding 14 d from the onset of the experiment revealed a decreased (P < 0.01) BUN concentration in LP (7.63 ± 1.07 mg/dL) compared with HP (18.81 ± 1.07 mg/dL) lambs. In addition, BUN concentrations 60 min postfeeding increased 1.75 ± 0.14 mg/dL relative to 30 min before feeding in HP lambs, whereas in LP lambs the increase was only of 0.87 ± 0.14 mg/dL (P < 0.001).

Blood urea N values reported in lambs of this age usually range between 7 and 12 mg/dL (Nikokyris et al., 1991; Sun and Zhou, 2010). These results were expected because, according to NRC (1985) recommendations, the LP diet was supposed to render lambs slightly undernourished in N (20% below requirements), and HP diet slightly overfed (33% above requirements).
Impact of Protein Supply and Feed Flavors on Preferences. The use of flavors allows separating diet selection based on nutrients from that based on hedonics (Villalba et al., 2011), and thus, it allows assessment of whether selection driven by nutrients or postgingestive effects is more important than selection driven by hedonics. For instance, Arsenos and Kyriazakis (1999) conditioned protein-deficient sheep to flavored feeds associated with incremental intraruminal doses of casein and showed that sheep were able to develop an aversion to protein and the aversion was also maintained when only the flavored feed was offered. During the 21 d of exposure to a flavor choice in 2 different buckets, lambs exposed to LP diets (LPC-LPU or LPC-LPM) on average consumed (1,020 ± 77.1 g/d) less (P < 0.01) total feed than those exposed to HPC-HPU or HPC-HPM diets (1,352 ± 77.1 g/d). As it occurred in the first 21 d of study, during this period there was a trend (P = 0.09) for HP lambs to progressively consume more feed than LP lambs (data not shown).

Overall, feed intake or animal performance was not directly affected by the flavor choice offered to lambs (Table 2). However, lambs receiving the LP diets finished the study with a decreased (P = 0.04) BW compared with those offered the HP diets. Accordingly, there were significant differences (P < 0.001) of ADG between CP levels, with LP lambs growing less than HP lambs. The poorer animal performance observed in lambs offered the LP diets was due to a combination of decreased (P = 0.01) total DMI and (P = 0.01) G:F of LP compared with HP lambs. Interestingly, there was an interaction (P < 0.001) between flavor choice and CP level. Lambs receiving LP diets with a choice of umami (LPC or LPU) consumed about the same amount of LPU feed as HP lambs presented with a choice of umami (HPC or HPU). In contrast, consumption of LPM was much less (P < 0.05) than that of HPM when offered simultaneously with an unflavored LP or HP diet, respectively. In fact, all lambs showed a preference for the plain diet (expressed as a percentage of total feed consumption) except for LP lambs offered the umami-flavored diet (LPU) as part of the 2-bucket choice between LPC and LPU.

Overall, the combination of 3 flavors was selected against (P < 0.01) at both CP levels, with an average

![Figure 1](image-url). Evolution of intake of lambs as affected by dietary CP. LP: low CP; HP: high CP (Exp. 1).
The objective of the first test of this experiment was to determine whether previous dietary CP level exposure would have preconditioning effects on the subsequent selection of LP or HP diets. The eating rate after 7 d of exposure was not different among treatments (data not shown). Likewise, there was no

Exp. 2: Diet Selection Based on Nutrient and Flavor Preferences

Test 1. The objective of the first test of this experiment was to determine whether previous dietary CP level exposure would have preconditioning effects on the subsequent selection of LP or HP diets. The eating rate after 7 d of exposure was not different among treatments (data not shown). Likewise, there was no

Impact of Protein Supply and Feed Flavors on Eating Behavior. Eating pattern was similar for lambs in LP and HP diets. However, an interaction between day and time (or hour) of sampling was found ($P < 0.05$) for eating pattern (Figure 3). Eating rate ($g/h$) was greatest 1 h after feeding. At 1 h after feeding, eating rate was greater ($P < 0.05$) for HP than for LP, whereas during the remaining measured times, eating rate was similar between the 2 CP levels except for 7 h after feeding, when lambs fed HP showed greater eating rates than lambs fed LP (Figure 3).

During the first day of offering the choice between plain and flavored diets, eating patterns did not differ ($P = 0.48$) between dietary CP levels, but they did change ($P < 0.05$) with flavor type. There were 2 marked peaks of feed consumption coinciding with 1 and 9 h after feeding, and there was 1 peak at 4 h after feeding for lambs exposed to a choice between LP and LPU (Figure 4). However, 4 d after offering the choice between plain and flavored diets, no effects ($P = 0.52$) of flavor or CP level were observed on eating pattern (Figure 4). The peak at 4 h observed with LPU on d 1 disappeared, and the eating rate for the remaining time points was similar to d 1 (Figure 4). These results further reinforce the idea that the enrichment of a low-CP diet with umami flavor was initially associated by lambs with an improved CP supply, but as time progressed and N supply remained largely unchanged, the initially elicited response (i.e., increased feed intake) extinguished over time.

Table 2. Intake and performance of lambs as affected by CP level and flavor of the diet (Exp. 1)

<table>
<thead>
<tr>
<th>Item</th>
<th>Low protein</th>
<th>High protein</th>
<th>$P$-value$^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Item</td>
<td>Umami</td>
<td>Mixture$^2$</td>
<td>Mixture$^2$</td>
</tr>
<tr>
<td>Initial BW, kg</td>
<td>35.4</td>
<td>33.9</td>
<td></td>
</tr>
<tr>
<td>Final BW, kg</td>
<td>35.9</td>
<td>34.8</td>
<td></td>
</tr>
<tr>
<td>ADG, g/d</td>
<td>67.3</td>
<td>41.9</td>
<td></td>
</tr>
<tr>
<td>Total intake (plain plus flavor), g/d</td>
<td>1,127.2</td>
<td>922.2</td>
<td></td>
</tr>
<tr>
<td>Intake of flavored feed, g/d</td>
<td>740.2$^b$</td>
<td>285.7$^b$</td>
<td></td>
</tr>
<tr>
<td>Intake, % of total consumption</td>
<td>71.6$^a$</td>
<td>30.6$^a$</td>
<td></td>
</tr>
<tr>
<td>Feed efficiency, %</td>
<td>6.4</td>
<td>4.4</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ Different superscripts within a row differ at $P < 0.05$.
$^b$ CPL: CP level effect; FT: flavor type effect; CPL×FT: interaction between CP level and flavor (umami or mixture of umami, sweet, and bitter).
$^c$ A flavor mixture composed of equal parts of umami, sweet, and bitter.

Preferedence of 39.9% of total feed consumption. Interestingly, the umami flavor was slightly selected against in HP but clearly selected (about 70% of total feed consumption) in favor ($P < 0.05$) with LP diets (Table 2). Lambs only showed a clear preference for LPU, with an average well above 50% of total feed consumption (Table 2). Moreover, lambs on the LP diet showed a preference for umami (LPU) even on the first day of testing, when the flavor was novel for them (Figure 2), but as the number of exposure days increased, LPU preference progressively decreased ($P < 0.01$). In contrast to this behavior, ruminants almost invariably eat only a small amount of a feed or flavor when it is offered for the first time (Chapple and Lynch, 1986; Chapple et al., 1987).

It is reasonable to hypothesize that protein-deficient lambs overcame the hesitation associated with a novel feed and consumed even greater amounts of flavored than unflavored feed initially as a consequence of the nature of umami oro-sensorial characteristics, which have been proposed to signal the presence of protein-bound compounds in feeds (Kurihara, 1987; Luscombe-Marshal et al., 2008; Beauchamp, 2009).

Collectively, the results herein provide evidence that lambs are able to detect umami flavor in a feed, associate it with protein, and increase the preference (and consumption) of that feed. However, the increase in consumption as an attempt to fulfill protein requirements progressively disappeared over time most likely due to an interaction with metabolic control of intake elicited by the absence of a concomitant supply of AA. A recent study (Favreau et al., 2010) has reported that lambs have a clear preference (about 80%) for hay sprayed with monosodium glutamate (umami) over the same hay without flavor, with little variation among individuals. The same authors showed that postigestive effects could be associated by lambs to the umami flavor in a way that lambs exposed to negative postigestive effects would actually lose their preference for umami. Thus, it is possible that in the current study, the lack of reward (i.e., lack of increased protein supply) associated with the consumption of umami-flavor feed reduced the innate preference that lambs seem to have for this taste. In contrast, flavor preferences
effect ($P = 0.15$) of previous dietary CP level (HP or LP) on total feed intake, although lambs previously exposed to HP consumed more ($P < 0.05$; Table 3) feed per day and tended ($P = 0.09$) to have greater intakes as a proportion of BW than LP lambs.

When offered HP and LP simultaneously, lambs previously exposed to LP diets progressively ($P < 0.01$) increased total daily intake throughout the test, whereas the amount of feed consumed by lambs previously exposed to HP diets remained unchanged (Figure 5). This observation further reinforces the notion that limiting CP supply compromises intake. Furthermore, on average, there were no differences ($P = 0.35$) in preferences for LP, which accounted for about 47% of total feed consumption (Table 3). However, there was a clear interaction between time and preference for the LP diet depending on previous exposure to dietary CP level (Figure 5). During the first day of testing, lambs that had initially received HP showed a reduced ($P < 0.05$) preference for LP ($23 \pm 2.05\%$) compared with lambs previously exposed to LP ($30 \pm 2.05\%$), but preference for LP rapidly increased in all lambs reaching a maximum at d 4 and then stabilizing around 50% at d 7 with no differences between treatments. These results suggest that, contrary to observations reported by Tolkamp et al. (1998) where dairy cows were not able to balance their diet according to protein needs and supply, lambs herein selected and mixed 2 foods to reach an equivalent CP concentration of about 15.7% of the DM consumed, which is close to the recommended dietary CP concentration for this type of lamb (NRC, 1985).

**Test 2.** The objective of this test was to evaluate the relationship between CP supply and preference for bitter taste. Lambs in the LP group consumed less ($P < 0.01$) feed than lambs in the HP group (Table 4) with
no interaction \((P = 0.22)\) between CP level and flavor. However, there was an interaction \((P < 0.01)\) between CP level, flavor, and day of testing on feed preferences. Basically, at the beginning of the test, preference for bitter or plain was about 50% for both CP levels, but as time elapsed, HP lambs continued to show no clear preference for either plain or bitter, whereas LP lambs progressively reduced the preference for the bitter taste from 53.0 ± 7.4% on d 1 to 34.1 ± 7.4% on d 7 (data not shown). A recent study (Favreau et al., 2010) also has reported that lambs showed neither preference nor aversion for bitter taste. However, the interaction between bitter, CP level, and day of testing observed herein supports the concept that bitter plays a role in the adaptive behavior, which has evolved as a way to facilitate avoidance of toxic foods (Garcia and Hankins, 1975; Glendinning, 1994). It is likely that a reduced preference for bitter by protein-restricted lambs represents the negative effects of bitter and its link with feed rejection (Temussi, 2009).

The eating rate of lambs participating in this test tended \((P = 0.08)\) to be slower when consuming LP than when consuming HP, but no interaction was observed with the presence of bitter (data not shown).  

**Test 3.** The objective of this test was to evaluate the relationship between protein supply and preference for sweet taste elicited by sucrose or a noncaloric sweetener. There were no overall differences in intake between CP amounts (Table 5). However, the interaction between CP amount and choice (sucrose vs. sweet) was significant \((P < 0.05)\) because lambs receiving LP diets consumed less concentrate with sucrose and even less with sweet flavor than plain, whereas lambs offered the HP diets consumed more concentrate with either sweet flavor or sucrose than plain. This response is in agreement with the hypothesis that animals tend to make dietary choices that minimize postingestive discomfort (Forbes, 2007). That is, in the current study, LP limited protein supply, and thus, under this hypothesis, lambs tended to avoid sucrose because this would have caused a more pronounced imbalance between energy and protein supply. However, it is likely that the dose of sucrose used (about 3 g/d) was not sufficiently large to alter energy supply, but still sufficient to alter palat-
ability. Interestingly, LP lambs clearly refused the non-caloric sweetener, which at the dose used (0.066%) was probably more noticeable than sucrose. This finding supports the idea that lambs attempted to avoid discomfort by rejecting a feed containing a flavor associated with energy supply. The response by lambs fed the HP diets is also in agreement with this hypothesis. Because HP diets provided an excessive supply of protein (and thus a mild energy deficit), lambs consumed more ($P < 0.05$) feed with either sucrose or sweetener in an attempt to correct the imbalance between CP and energy (Table 5). These responses are more evident in terms of feed preferences, given that lambs preferred LP plain over the LP concentrates with sweetener or sucrose.

Figure 4. Evolution of eating rate of lambs throughout 9 h after feeding as affected by CP level and flavor after different days of exposure to the diets. LPC: plain low CP; HPC: plain high CP; LPU: low CP plus umami; HPU: high CP plus umami; LPM: low CP plus a mixture of 3 flavors; HPM: high CP plus a mixture of 3 flavors (Exp. 1).
Table 3. Intake and choice between high (HP) or low (LP) CP diets as affected by previous dietary CP level exposure in lambs (Exp. 2)

<table>
<thead>
<tr>
<th>Item</th>
<th>Previous CP level</th>
<th>P-value$^1$</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LP</td>
<td>HP</td>
<td>SE</td>
<td>CPL</td>
<td>Day</td>
</tr>
<tr>
<td>Total intake, g/d</td>
<td>1,172</td>
<td>1,392</td>
<td>101</td>
<td>0.15</td>
<td>0.01</td>
</tr>
<tr>
<td>Intake, % of BW</td>
<td>3.16</td>
<td>3.71</td>
<td>0.22</td>
<td>0.09</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Intake of LP, % of total consumption</td>
<td>47.1</td>
<td>46.8</td>
<td>4.6</td>
<td>0.35</td>
<td>0.99</td>
</tr>
</tbody>
</table>

$^1$CPL: CP level effect; CPL × day: interaction between CP level and day of study.

Table 4. Consumption and preferences for feeds unflavored or bitter-flavored as affected by dietary CP level in lambs (Exp. 2)

<table>
<thead>
<tr>
<th>Item</th>
<th>Low CP</th>
<th>High CP</th>
<th>P-value$^1$</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Plain</td>
<td>Bitter</td>
<td>Plain</td>
<td>Bitter</td>
<td>SE</td>
<td>CPL</td>
</tr>
<tr>
<td>Total intake, g/d</td>
<td>520</td>
<td>373</td>
<td>725</td>
<td>783</td>
<td>82.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Intake, % of BW</td>
<td>2.63</td>
<td>2.62</td>
<td>3.79</td>
<td>3.79</td>
<td>0.28</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Intake, % of total consumption</td>
<td>57.2</td>
<td>42.8</td>
<td>49.2</td>
<td>50.8</td>
<td>6.3</td>
<td>0.99</td>
</tr>
</tbody>
</table>

$^1$CPL: CP level effect; FT: flavor type effect; CPL × FT: interaction between CP level and flavor (plain vs. bitter).

Figure 5. Total feed intake (g/d) and preference for a low CP (LP) diet (as a percentage of total feed intake) when lambs previously exposed to either a high CP (HP) or an LP diet were offered a simultaneous choice of both (LP and HP) diets (Exp. 2).
that signals the presence of CP in feed. These behav-
ioral nutrient imbalances as they increase their prefer-
ence for a feed high in CP (HP) or a flavor (umami)
whereas HP lambs preferred the HP concentrates with
sweetener or sucrose over the plain HP concentrate. It
is interesting to note that the interaction between CP
amount, choice, and time was not significant, and thus
feed preferences were rapidly established by lambs since
the first day of testing.
In summary, a cross-talk between umami, bitter, and
sweet receptors has been proposed (Tenussi, 2009).
For instance, umami taste may enhance the perception and
preference for other tastants as most presynaptic
taste cells respond to 2 or more different taste qualities
(Tomchik et al., 2007). Results from this experiment
suggest that when these taste qualities are presented
together in a mixture (Exp. 1), such enhancement does
not take place. That is, the consumption of LPU, but
not LPM, increased in protein-restricted lambs. In addi-
tion, consumption of LPU did not differ from HPU,
whereas intake of LPM was much less than intake of
HPM for lambs exposed to low CP and high CP diets,
respectively. When bitter and sweet flavors were tested
separately (Exp. 2), lambs fed the low CP diet also
showed reduced intake and preferences for these flavors
relative to lambs offered the HP diet. Thus, responses of
the lambs to the mixture of flavors under protein re-
striction seem to be driven by the inhibitory effects of
bitter and sweet over the stimulatory effects of umami.

Protein-restricted lambs seem capable of sensing di-
etary nutrient imbalances as they increase their prefer-
ence for a feed high in CP (HP) or a flavor (umami)
they are offered the appropriate feed alternatives. The
presence of the umami flavor in feeds may provide cues
that help protein-deficient animals overcome neophobia
and direct their selection and intake to such feeds in
relatively short periods of time. In contrast, the pres-
ence of sweet or bitter flavors in protein-deficient diets
may provide cues that reduce acceptance of such diets
beyond what is expected by the sole negative effects of
the imbalance.

Table 5. Consumption and preferences for feeds either unsupplemented or containing sucrose or a sweet flavor as
affected by dietary CP level in lambs (Exp. 2)

<table>
<thead>
<tr>
<th>Item</th>
<th>Low CP</th>
<th>High CP</th>
<th>P-value&lt;sup&gt;1&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Plain</td>
<td>Sucrose</td>
<td>Sweet</td>
</tr>
<tr>
<td>Intake, g/d</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>948&lt;sup&gt;a&lt;/sup&gt;</td>
<td>501&lt;sup&gt;b&lt;/sup&gt;</td>
<td>292&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
| Intake, % of total con-
sumption                   | 80.0<sup>y</sup> | 33.0<sup>y</sup>| 25.0<sup>y</sup>    |      |      |      |          |

<sup>a</sup>Different superscripts within a row differ at <i>P</i> < 0.05.
<sup>1</sup>CPL: CP level effect; FT: flavor type effect; CPL × FT: interaction between CP level and flavor (sucrose vs. sweet).

LITERATURE CITED

tioned flavor preference and acceptance in rats: Effects of de-
privation state and nonreinforcement. Physiol. Behav. 56:701–
707.
Favreau, A., R. Baumont, G. Ferreira, B. Dumonta, and C. Ginane. 2010. Do sheep use umami and bitter tastes as cues of post-
Forbes, J. M. 1977a. Interrelationships between physical and meta-
bolic control of voluntary food intake in fattening, pregnant
Forbes, J. M. 1977b. Development of a model of voluntary food
Forbes, J. M. 2007. A personal view of how ruminant animals control
their intake and choice of food: Minimal total discomfort. Nutr.
Galloun, F., and J. Le Magnen. 1987. Évolution historique des con-
acquisition of toxiphobia. Pages 39–45 in Olfaction and Taste: Pro-
cedings of the 5th International Symposium. D. A. Denton
Glendinning, J. I. 1994. Is the bitter rejection response always adap-
Nutrient and taste interactions


