



How the foraging decisions of a small ruminant are influenced by past feeding experiences with low-quality food



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ABSTRACT

Feeding experiences with low-quality foods can be improved when these foods are ingested in close temporal association with foods of higher nutritional quality. However, preference for low-quality foods in nature seems to be rather insensitive to past positive experiences and more related to their intrinsic nutritional value. An explanation for this observation is still lacking, mainly because little is known about how herbivores use information about low-quality foods during foraging. Our objective was to provide original information about this issue using a small ruminant (sheep; *Ovis aries*) as animal model. We manipulated the sheep's experience with a low-quality food (wheat straw) using a conditioning procedure ("oral-delay conditioning procedure"), and then we evaluated the use of this information in a simulated foraging scenario provided with wheat straw and a variable amount of a high-quality food in spatially separated feeding stations. Inclusion of wheat straw into the diet was strongly dependent on the availability of the high-quality food. We observed a threshold level in the availability of the high-quality food, which defined a zone of drastic change in the likelihood of inclusion of the wheat straw into the diet (i.e., acceptance or rejection of wheat straw). This threshold level did not change for sheep with (CS+) or without (CS-) a previous positive experience with wheat straw. However, once foraging conditions stimulated all sheep to start including the wheat straw into the diet (i.e., below the threshold level), the intake of this food was greater by CS+ sheep. This increased intake was not explained by a higher motivation to eat the wheat straw but to a greater amount of time spent foraging this food and less time spent searching for the preferred higher-quality alternative. We discuss these results based on optimal foraging models and learning models of diet selection.

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Food selection by generalist mammalian herbivores is expected to be flexible in response to the constant and unpredictable spatiotemporal variation in food quality and quantity, as these variables directly impact a consumer's fitness (Provenza and Villalba, 2006). Animals gather information from the environment to adjust foraging decisions to complex and ever-changing situations (Fawcett et al., 2014). In this regard, the study of foraging behaviour seeks to unveil the types of information that are important to the consumer (e.g., nutritional quality of foods, food distribution and scale, variance of availability) (Senft et al., 1987; Simpson et al., 2004) and how animals integrate and process this information to make foraging decisions (e.g., Houston et al., 2011).

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Actual dietary choices are influenced by previous feeding experiences (Zhang and Hui, 2014). Mammalian herbivores have the ability to learn from the post-ingestive consequences of foods, which allow them to balance nutrient intake according to their current physiological needs (i.e., learning model of diet selection; Provenza, 1995; Provenza and Cincotta, 1993). Foods associated with the provision of nutrients that satisfy nutritional requirements are accepted, while foods with nutritional limitations (i.e., low-quality foods) are commonly rejected (O'Reagain and Grau, 1995). However, preferences for low-quality foods are not only influenced by their own intrinsic nutritional value but also by the nutritional context in which these foods are ingested (e.g., Baraza et al., 2005). For instance, lambs show greater intake of a flavoured wheat straw when the ingestion of this low-quality food is immediately followed by a nutritious meal than when the ingestion of wheat straw is temporally isolated from that nutritious meal (Freidin et al., 2012, 2011); also called the "oral-delay conditioning procedure" (Sclafani, 1995). Thus, one corollary of the learning

model of diet selection is that the incentive value of a low-quality food – and thus its preference – can increase through conditioning by pairing the low-quality food with a high-quality feeding environment. In support of this, the manipulation of feeding experiences through conditioning procedures has consistently changed animals' preference for low-quality foods in experimental settings (e.g., Villalba and Provenza, 1999). However, similar conditioning procedures have shown limited success at modifying herbivores' responses to low-quality foods in natural situations (e.g., Whitney and Olson, 2007). Rules that govern decision-making in the environment to which an animal has been adapted may not be properly expressed in artificial laboratory settings (Bateson, 2004). In nature, the food environment is inherently diverse, with forages of different abundances and nutritional composition and variable spatial distribution (Senft et al., 1987). In contrast, controlled conditioning procedures involve free-choice trials among foods of similar nutritional composition, located in close proximity to each other and with ad libitum availability (e.g., Pérez et al., 1995). Thus, access to foods of contrasting nutritional composition, and the time and effort required to harvest them from the environment could be key variables – not considered in free-choice trials – involved in the expression of previously acquired conditioned preferences for low-quality foods (see Catanese et al., 2015 for a preliminary study).

The optimal foraging theory (OFT) recognizes environmental constraints (e.g., search and exploitation restrictions) and gives a functional approach to the analysis of foraging behaviour (Stephens and Krebs, 1986). One of the predictions is that herbivores' decision to include a low-quality food in the diet is not only influenced by its own value but also by the availability and profitability of higher-quality options. This suggests that increases in the incentive value (i.e., the subjective learned value of a given food) of a low-quality food (e.g., through a conditioning procedure) may not necessarily be translated into a higher preference for this food while foraging, because preference for low-quality foods depends on the contextual situation provided by higher-quality alternatives. Thus, while learning models of diet selection commonly disregard contextual constraints that are likely to influence foraging decisions (e.g., availability, access and distribution of feeding options), OFT models overlook the role that learning and previous experiences have on the determination of the incentive value of foods (e.g., the influence of the nutritional context in which a certain food was previously ingested) (but see McNamara et al., 2006). The integration of both models could contribute to better explaining the foraging decisions made by herbivores in nature.

We hypothesized that during foraging sheep use previously learned information about a low-quality food according to optimal foraging rules. Our approach was to investigate how previous experience with a low-quality food influences the dynamics of foraging decisions made by sheep when the availability of a high-quality food in different feeding stations is manipulated. According to OFT models, animals should include foods of low-quality into their diets depending on how profitable it is to forage higher-quality options. For instance, above a certain threshold level of profitability from feeding on a high-quality food, the optimal solution for a consumer is to avoid lower quality alternatives (Focardi et al., 1996) in order to maximize the rate of nutrient intake (Illius et al., 1999). Below the threshold level, feeding exclusively on the high-quality food is less profitable than also including the low-quality food into the diet, and therefore, the low-quality food should be accepted when encountered. We also predicted that instead of being constant, the incentive value given by a consumer to a low-quality food is variable and dependent upon the consumer's previous feeding experiences with that food. Based on traditional learning models of diet selection (Provenza, 1995) we consider that following a positive experience a low-quality food (e.g., as a product of a preference conditioning procedure) will be ranked better (i.e., will increase its

perceived profitability) than if we consider a regular experience with this low-quality food (i.e., without conditioning). Therefore, we reasoned that according to OFT models sheep with a positive previous experience with the low-quality food are expected to start including the low-quality food into their diet at a higher level of availability of the high-quality food, compared with sheep with a regular experience with the low-quality food.

1. Methods

The study was conducted at the “Centro de Recursos Naturales Renovables de la Zona Semiárida” (CERZOS) located in Bahía Blanca (38°44'S; 62°16'W), Argentina, from April 2013 to November 2013. All experimental protocols fulfilled the animal welfare regulations of the Universidad Nacional del Sur (Bahía Blanca, Argentina) and adhered to the ASAB/ABS (2012) guidelines for the use of animals in research and teaching. Throughout the study, the sheep had free access to water and trace mineral salt blocks.

1.1. Animals, housing, and training phase

Twenty-four 2-year-old female Merino sheep (*Ovis aries*; 46.7 ± 3.68 kg live weight [LW] [mean \pm SD]) were kept as a group in a protected enclosure (20 \times 20 m) and fed to maintenance with vegetative grass hay (hereafter, “pasture hay;” crude protein [CP]: 12.4 g/100 g, neutral detergent fibre [NDF]: 62.5 g/100 g, mean particle size: 15 mm) at 1700 h.

Sheep were exposed to a training phase in a U-shaped corridor (hereafter, “corridor;” see Catanese et al., 2015) to familiarize them with the facilities and to allow them to learn the experimental procedure that was later used during testing. The corridor (15 m \times 6 m, length \times width) was built with black canvas walls (1.5 m high) with an entrance gate on both ends and a pair of plastic buckets (30 cm \times 50 cm, length \times width, and 20 cm high) at both ends. The buckets had two equal inner compartments (15 cm \times 25 cm, length \times width) and were large enough to allow a pair of sheep to eat from the same bucket with minimal interference (Lynch et al., 1992).

Training sessions were conducted daily from 0800 h to 1200 h for 15 consecutive days. Because sheep are reluctant to eat in isolation (Sibbald and Hooper, 2004), they were trained in randomly selected pairs, blocked by LW. The same pairs of sheep were maintained throughout the experiment. During training sessions, a pair of sheep was taken at random and walked into the corridor through either of the two entrance gates. Once inside the corridor, they were fed ground oat grain (CP: 11.9 g/100 g, NDF: 33.0 g/100 g, mean particle size: 2 mm) at 0.032% of LW (mean LW of the pair) in each inner compartment of one of the feed buckets at both ends of the corridor. After sheep ate all of the oat grain at one end of the corridor, we waited 3 min to determine if they voluntarily moved to the other end of the corridor; if not, we walked them gently into that direction. Once the sheep started feeding at the new location, we refilled oat grain in the previous one. Food was always provided by the same operator through a small window located in the wall behind the feed buckets; the sheep were not able to see when food was refilled or when the operator was performing the procedure. We ran this protocol until sheep voluntarily moved from one end of the corridor to the other at least five times. Once the training session was completed, we opened the gate closest to the animals' location, allowing the pair to return to the communal enclosure. The same procedure was repeated until all pairs of sheep had undergone their daily training session. By the end of the training phase, all pairs of sheep successfully moved from one end of the U-shaped corridor to the other without human intervention.

1.2. Treatments and conditioning phase

The day after the training phase ended, all sheep were weighed and individually penned (in adjacent wooden pens of 2.5 m × 2.5 m each) outdoors under a protective roof. The sheep were allowed to familiarize themselves with the new experimental conditions for seven days, and during this time, they were fed pasture hay at 2.5% of LW/d.

After familiarization, sheep were randomly assigned to one of two treatments (12 sheep/treatment): (1) exposition to a preference conditioning protocol with a low-quality food (conditioned sheep, CS+), or (2) simple exposition to the low-quality food (control sheep; CS-). There were two restrictions on randomization: animals from the same pair were kept in the same treatment, and treatments were balanced by LW. The conditioning phase lasted for 15 consecutive days.

Daily conditioning sessions were run from 0900 h to 1000 h, and started by offering all sheep a bucket (similar to that used in the corridor) containing ad libitum amounts of ground wheat straw (low-quality food; CP: 3.2 g/100 g, NDF: 84.6 g/100 g, mean particle size: 10 mm) for 20 min (0900 h to 0920 h). Then, sheep in CS+ were offered a bucket with 0.4% LW of ground soybean meal (hereafter, “soybean;” high-quality food; CP: 42.5 g/100 g, NDF: 13.5 g/100 g, mean particle size: 2 mm) for 30 min (0930 h to 1000 h), whereas sheep in CS- received an empty bucket for the same period of time. In the afternoon (1600 h), all animals were fed pasture hay at 2.5% of LW. Additionally, sheep in CS- were fed soybean at 0.4% of LW to compensate for the type and amount of food offered daily to sheep in CS+ during conditioning.

1.3. Testing phase

The objective of this phase was to assess the sheep’s foraging behaviour as a function of their previous experiences with wheat straw and the level of availability of a high-quality food in the foraging environment.

Sheep were exposed to two different high-quality foods in two consecutive periods: alfalfa pellets (hereafter, “alfalfa;” CP: 14.1 g/100 g, NDF: 45.0 g/100 g, mean particle size: 10 mm) in Test 1, and corn grain (hereafter, “corn;” CP: 8.9 g/100 g, NDF: 10.4 g/100 g, mean particle size: 2 mm) in Test 2. Because corn has a higher nutritional quality than alfalfa for sheep (National Research Council, 1985), it allowed us to test the animal’s foraging decisions across a gradient of nutritional qualities: corn > alfalfa > wheat straw. Sheep prefer grain over alfalfa (Scott and Provenza, 1999), and both alfalfa and corn are strongly preferred over oat straw (a low-quality food similar to wheat straw) (Catanese et al., 2010).

Sheep were tested in the corridor following the same protocol used for the Training Phase, except that the duration of daily sessions was limited to 15 min and sheep were never forced to move inside the corridor. At both ends of the corridor, one bucket contained 30 g of wheat straw per inner compartment, and the other bucket contained the high-quality alternative (alfalfa or corn) at one of eight levels of availability (2, 4, 6, 8, 12, 16, 24, or 32 g) per inner compartment. The amounts of high-quality food offered were chosen based on a previous work, which suggested these levels represent a sensitive range of high-quality food restriction for sheep (Catanese et al., 2015). The amount of wheat straw was selected based on preliminary research and it allowed a minimum level of 10% refusals during each visit to the buckets. During daily testing sessions, sheep never ate more than 1/3 of their nutritional requirements (National Research Council, 1985), which reduced the likelihood of digestive constraints acting as a confounding factor. The position of the foods in the buckets was randomly assigned between the pair of buckets located at both ends of the corridor on a daily basis. Once the alfalfa or corn was depleted, animals were

free to decide whether to stay and eat wheat straw or go to the other end of the corridor to eat more alfalfa or corn. Similar to Training Phase, once the sheep started feeding at the new location, we refilled the high-quality food and the wheat straw in the previous one. All pairs of sheep were randomly exposed to each level of high-quality food availability in periods of four consecutive days. Between periods of different high-quality food availability, sheep were kept in individual pens and exposed to the same protocol described for the Conditioning Phase for three consecutive days (hereafter, “inter-testing conditioning”). This procedure was performed to avoid potential carry-over effects due to exposure to wheat straw without conditioning during successive tests.

Two video cameras (Foscam FI8904W, ShenZhen Foscam Intelligent Technology Co., Shenzhen, China) were set in the corridor to obtain recordings at 30 frames per second (i.e., real-time) of sheep behaviour during each testing session.

1.4. Chemical analyses of feeds

All feeds used during the study were sampled each time before feeding, composited for seven days and then prepared for chemical analyses. Composited samples were dried for 48 h at 60 °C, ground through 1-mm mesh, and analysed for crude protein (AOAC, 2002; Method 990.03) and NDF (without the addition of sodium sulphide; Van Soest et al., 1991).

1.5. Measurements and statistical analyses

Wheat straw, alfalfa, and corn intake were calculated as the difference between dry matter offered and dry matter refused. Left-overs were quantified each time sheep moved from one end to the other end of the corridor. Video recordings were analysed for the last two sessions of each level of alfalfa or corn availability, when sheep had the greatest level of exposure to the conditions of the test. Recorded activities of individual sheep were scan sampled at 15-s time intervals (Martin and Bateson, 1993), and categorized as: 1-eating wheat straw, 2-eating alfalfa (or corn), 3-walking, or 4-involvement in other activities (hereafter, “idling”). Feed intake rate was calculated as the mean amount of food eaten by the pair of sheep during each visit to the buckets at one end of the corridor divided by the mean amount of time spent by the pair of sheep eating the corresponding food during the same visit.

Statistical analyses were performed using the R environment (R Core Team, 2012). Model diagnostics included testing for normal distribution, homogeneity of variance, and linearity. Least square means and standard errors were obtained with the “lsmeans” package (Lenth, 2012). All data are reported as the means ± 1 SEM. Contrasts between variables were performed using Tukey’s HSD test.

Wheat straw intake data during conditioning and inter-testing conditioning sessions were analysed separately with a mixed effects model (Pinheiro et al., 2012). The model included treatment (CS+ and CS-), day, and treatment × day interaction as fixed effects, and sheep as random effects. The model was fitted with an autoregressive order-1 covariance structure (Chi-square test: $X_1 > 39.9$, $P < 0.001$ for all analyses).

Data on feed intake and feed intake rate during testing sessions were averaged over the last two days of testing. These data were fit with a linear and a nonlinear model (logistic model, “nlme” package; Pinheiro et al., 2012) to evaluate goodness of fit, and analysed separately for each level of availability of alfalfa or corn. The logistic model was selected, among other possible models, because inclusion of the lower-quality food alternative in the diet is commonly related to the profitability of a higher-quality food alternative by an “S-shaped” (Stephens, 1985) or a sigmoid-like function (e.g., Dumont et al., 1998). Models included treatment, level of avail-

ability of either alfalfa or corn, and treatment \times level of availability of alfalfa or corn as fixed effects, and the pair of sheep as random effects.

Data on the proportion of scans in which sheep were eating wheat straw, alfalfa or corn, walking, and idling during the testing phase, were averaged over the last two days of each level of availability of alfalfa or corn. These data were fit with a linear and a nonlinear (logistic) model to evaluate goodness of fit. Models included treatment, level of availability of alfalfa or corn, and treatment \times level of availability of alfalfa or corn as fixed effects, and the pair of sheep and individual sheep nested within each pair of sheep as random effects.

2. Results

2.1. Conditioning phase and inter-Testing conditioning phase

During the conditioning phase, all sheep gradually increased wheat straw intake ($F_{1,334} = 14.14$, $p < 0.001$, data not shown) until the last 5 days of testing, when no differences were observed among days ($F_{1,334} = 0.21$, $p = 0.645$). Mean wheat straw intake during this phase was similar between sheep in CS+ and sheep in CS- (157.0 versus 137.2 \pm 11.91 g/session, respectively; $F_{1,22} = 1.46$, $p = 0.240$); however, the increase in wheat straw intake in this phase was faster in sheep in CS+ than sheep in CS- (treatment \times sessions interaction, $F_{1,334} = 4.23$, $p = 0.040$). At the end of the conditioning phase, LW was similar between CS+ and CS- (46.0 versus 46.9 \pm 1.11 kg, respectively; $F_{1,22} = 0.37$, $p = 0.549$).

During the inter-testing conditioning phases of Test 1 and Test 2 (see below), intake of wheat straw was similar across days ($F_{1,46} = 0.31$, $p = 0.581$), and similar between sheep in CS+ and sheep in CS- (208.6 versus 199.6 \pm 12.6 g/session, respectively; $F_{1,22} = 0.26$, $p = 0.612$).

2.2. Testing phase

2.2.1. Test 1—Alfalfa

2.2.1.1. Food intake. Fig. 1a summarizes wheat straw intake during Test 1. The intake of wheat straw showed a nonlinear relationship with alfalfa availability (linear model adjusted to data predicted negative intake of wheat straw for the two highest levels of alfalfa availability). Fitting a logistic model to the data showed lower AIC (Akaike Information Criterion) than fitting a linear model. Treatment had a significant impact on the parameter representing the asymptote of the model ($t(129) = 3.21$, $p = 0.002$), accounted for by the greater value for the asymptote for sheep in CS+ than sheep in CS- (241.6–330.6 g/pair versus 151.3–240.1 g/pair, 95% confidence limits; respectively). The parameter representing the threshold level of alfalfa availability were behaviour towards the wheat straw changed (i.e., the inflection point of the logistic curve) was not affected by treatments (8.9–11.5 g versus 4.8–15.6 g, 95% confidence limits; for sheep in CS+ and sheep in CS- respectively). Evaluation of wheat straw intake at each level of alfalfa availability with a linear mixed model showed that intake was greater for sheep in CS+ than sheep in CS- when alfalfa availability was below the threshold level suggested by the logistic model (10.18 \pm 0.87 g, mean \pm SE).

Mean alfalfa intake, analysed with a linear mixed model, was greater for sheep in CS- than sheep in CS+ (460.6 versus 337.4 \pm 32.3 g/pair, respectively; $F_{1,10} = 5.29$, $p = 0.044$; Fig. 2a). Treatment \times alfalfa availability interaction was not significant ($F_{1,166} = 1.68$, $p = 0.196$).

2.2.1.2. Behaviour. The total amount of time sheep spent eating wheat straw showed a nonlinear increase with decreasing alfalfa availability (Fig. 3a). Fitting a logistic model to the data showed

lower AIC than fitting a linear model. Treatment had a significant impact on the parameter representing the asymptote of the model ($t(129) = 9.81$, $p < 0.001$). Time spent eating wheat straw, analysed with a linear mixed model at each level of alfalfa availability, was higher for sheep in CS+ than sheep in CS- when alfalfa availability was below the threshold level suggested by the logistic model (8.88 \pm 0.46 g, mean \pm SE).

The total amount of time sheep spent eating alfalfa showed a treatment \times alfalfa availability interaction ($F_{7,346} = 4.36$, $p < 0.001$; Fig. 3b). Compared with sheep in CS+, sheep in CS- spent more time eating alfalfa only when alfalfa availability was between 4 and 8 g.

The total amount of time sheep spent walking through the corridor showed a treatment \times alfalfa availability interaction ($F_{7,346} = 2.61$, $p = 0.012$; Fig. 3c). Compared with sheep in CS+, sheep in CS- spent more time walking only when the alfalfa availability level was lower than 8 g. The total amount of time spent idling was similar between sheep in CS+ and sheep in CS- (28.4 versus 38.3 \pm 6.3 s, respectively; $F_{1,10} = 0.96$, $p = 0.351$).

Intake rate of wheat straw was similar ($F_{1,90} = 0.02$, $p = 0.88$) among levels of alfalfa availability. The mean intake rate of wheat straw was similar between sheep in CS+ and sheep in CS- (0.22 versus 0.26 \pm 0.04 g/s, respectively; $F_{1,10} = 0.06$, $p = 0.806$). The intake rate of alfalfa was positively correlated with alfalfa availability (regression coefficient = 0.035 \pm 0.003, $F_{1,166} = 586.70$, $p < 0.001$, $R^2 = 0.72$). The mean intake rate of alfalfa was similar between sheep in CS+ and sheep in CS- (0.48 versus 0.44 \pm 0.03 g/s, respectively; $F_{1,10} = 0.83$, $p = 0.384$).

2.2.2. Test 2—Corn

2.2.2.1. Food intake. Fig. 1b summarizes wheat straw intake data during Test 2. Intake of wheat straw showed a nonlinear relationship with corn availability (linear model adjusted to data predicted negative intake of wheat straw for the two highest levels of corn availability). Fitting a logistic model to the data showed lower AIC than fitting a linear model. Treatment had a significant impact on the parameter representing the asymptote of the model ($t(129) = 4.91$, $p < 0.001$), accounted for by the greater value for the asymptote for sheep in CS+ than sheep in CS- (560.9–445.3 g/pair versus 400.5–284.9 g/pair, 95% confidence limits; respectively). The parameter representing the threshold level of corn availability were behaviour towards the wheat straw changed was not affected by treatments (2.5–8.5 g versus 0.1–6.2 g, 95% confidence limits; for sheep in CS+ and sheep in CS- respectively). Evaluation of wheat straw intake at each level of corn availability with a linear mixed model showed that intake was greater by sheep in CS+ than sheep in CS- when corn availability was below the threshold level suggested by the logistic model (4.83 \pm 1.49 g, mean \pm SE), although a higher intake of wheat straw by CS+ sheep was also detected when corn availability was 8 g.

Mean corn intake, analysed with a linear mixed model, was similar between sheep in CS+ and sheep in CS- (494.3 versus 526.4 \pm 24.4 g/pair, respectively; $F_{1,10} < 0.01$, $p = 0.960$; Fig. 2b). The treatment \times corn availability interaction was not significant ($F_{1,166} = 0.67$, $p = 0.413$).

2.2.2.2. Behaviour. The total amount of time sheep spent eating wheat straw showed a nonlinear increase with decreasing corn availability (Fig. 4a). Fitting a logistic model to the data showed lower AIC than fitting a linear model. Treatment had a significant impact on the parameter representing the asymptote of the model ($t(129) = 4.51$, $p < 0.001$). Time spent eating wheat straw, analysed with a linear mixed model at each level of corn availability, was higher for sheep in CS+ than sheep in CS- when corn availability was between 4 and 8 g; at the lowest level of corn availability, time spent eating wheat straw was the same between groups.

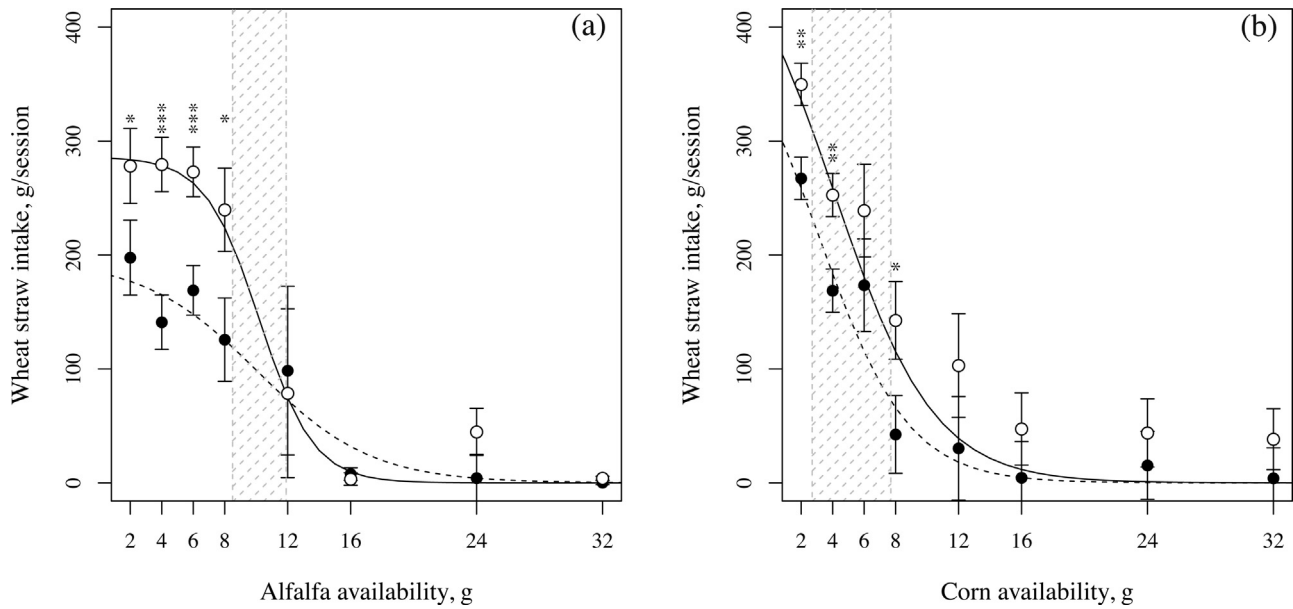


Fig. 1. Mean intake of wheat straw (± 1 SEM represented by error bars) by pairs of sheep either previously exposed (CS+, open circles) or not previously exposed (CS-, full circles) to a preference conditioning procedure during the last two sessions of testing in a foraging scenario in which the availability of alfalfa pellets (a) or corn grain (b) (i.e., high-quality foods) in each feeding site was restricted to 2, 4, 6, 8, 12, 16, 24, or 32 g/per animal. Lines represent the logistic adjustment for data from sheep in CS+ (solid line) and sheep in CS- (dashed line). Grey dashed lines delimit the zone (between 95% confidence limits) in which the inflection of the general logistic model (including both treatments) was estimated (also called threshold level in the text). Comparisons between treatments at each level of availability were performed using Tukey's HSD test. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

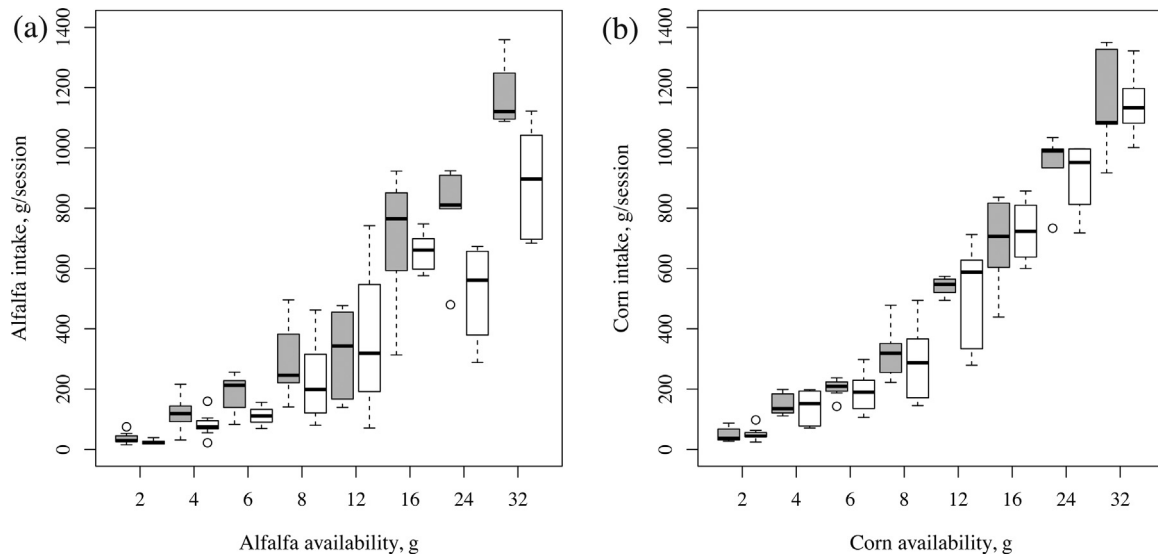


Fig. 2. Mean intake of alfalfa (a) and mean intake of corn (b) by pairs of sheep either previously exposed (CS+, white boxes) or not previously exposed (CS-, grey boxes) to a preference conditioning procedure during the last two sessions of testing in a foraging scenario in which the availability of alfalfa or corn, respectively, in each feeding site was restricted to 2, 4, 6, 8, 12, 16, 24, or 32 g/per animal. Box plots show the median (black line), the interquartile range (box), and the minimum and maximum value within 1.5 times the interquartile range of the box (whiskers) and outliers (circles).

The total amount of time sheep spent eating corn was similar between sheep in CS- and sheep in CS+ (453.3 versus 412.8 ± 29.9 s, respectively; $F_{1,10} = 0.03$, $p = 0.861$; Fig. 4b).

The total amount of time sheep spent walking showed a treatment \times corn availability interaction ($F_{7,346} = 2.36$, $p = 0.023$; Fig. 4c). Sheep in CS- spent more time walking through the corridor than sheep in CS+, but only when the alfalfa availability level was lower than 6 g. The total amount of time spent idling was similar between sheep in CS+ and sheep in CS- (22.5 versus 24.1 ± 1.4 s, respectively; $F_{1,10} = 2.23$, $p = 0.166$).

Intake rate of the wheat straw was similar ($F_{1,90} = 1.19$, $p = 0.280$) among levels of corn availability. The mean intake rate of wheat

straw was similar between sheep in CS+ and sheep in CS- (0.26 versus 0.29 ± 0.03 g/s, respectively; $F_{1,10} = 0.52$, $p = 0.486$). The intake rate of corn was positively correlated to corn availability (regression coefficient = 0.030 ± 0.002 , $F_{1,166} = 423.08$, $p < 0.001$, $R^2 = 0.83$). The mean intake rate of corn was similar between sheep in CS+ and sheep in CS- (0.44 versus 0.45 ± 0.02 g/s, respectively; $F_{1,10} = 1.12$, $p = 0.315$).

3. Discussion

Our results were in close agreement with the hypothesis that during foraging, sheep use previously learned information about a

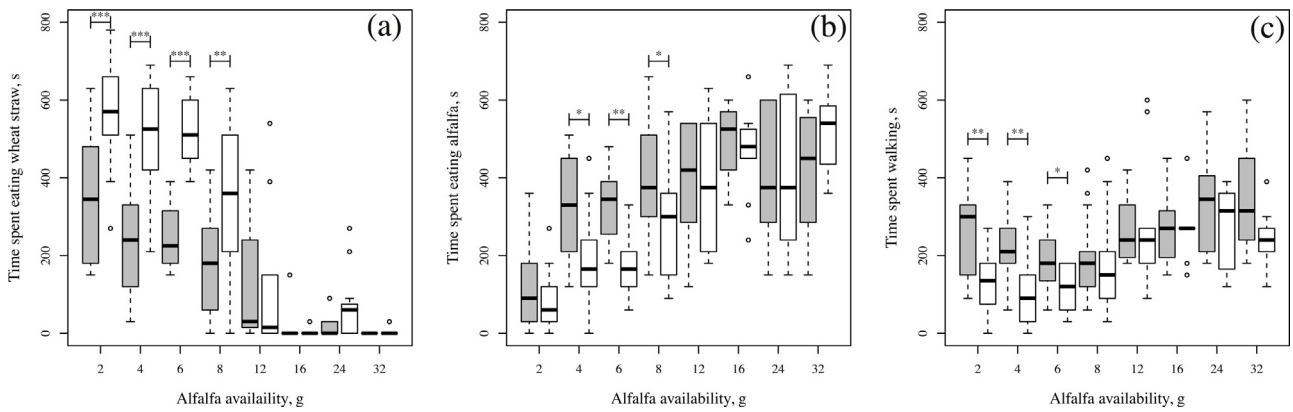


Fig. 3. Mean time spent eating wheat straw (a), mean time spent eating alfalfa (b), and mean time spent walking (c) by individual sheep either previously exposed (CS+, white boxes) or not previously exposed (CS-, grey boxes) to a preference conditioning procedure during the last two sessions of testing in a foraging scenario in which the availability of alfalfa in each feeding site was restricted to 2, 4, 6, 8, 12, 16, 24, or 32 g per animal. Box plots show the median (black line), the interquartile range (box), and the minimum and maximum values within 1.5 times the interquartile range of the box (whiskers) and outliers (circles). Comparisons between treatments at each level of availability were performed using Tukey's HSD test. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

low-quality food according to optimal foraging rules. Regardless of the type of conditioning treatment (CS+ or CS-), the likelihood of sheep including wheat straw in the diet was strongly influenced by the availability of high-quality food (alfalfa or corn). The observed nonlinear relationship suggests a threshold level in the availability of the high-quality food, which defines a shift zone in the foraging strategy displayed by sheep (i.e., to select or reject wheat straw). Below the threshold level of high-quality food availability, animals of both treatments started to eat wheat straw, but sheep in CS+ expressed their previous positive experiences with wheat straw by showing greater intake and enhanced behavioural responses to this food compared with sheep in CS-. However, sheep in CS+ did not start including wheat straw at higher levels of high-quality food availability, as was predicted. Possible explanations for the latter result are given below.

The occurrence of a threshold level in the availability of high-quality food at which foraging behaviour changed abruptly was also observed by Focardi et al. (1996) in fallow deer (*Dama dama*), Dumont et al. (1998) in sheep, Illius et al. (1999) in goats (*Capra hircus*), and Hirata et al. (2006) in cows (*Bos taurus*). Evidence in favour of this threshold is consistent with the “zero-one” rule (Stephens and Krebs, 1986) or the “all-or-none” choice (McNamara and Houston, 1987) predicted by OFT models. However, partial preferences were observed in our study, which may contest OFT

predictions (Provenza et al., 2003). Partial preferences are expected by OFT models (e.g., McNamara and Houston, 1987), especially if we consider that around the threshold level, the profitability of feeding options is very similar and animals may fail to discriminate between options (Illius et al., 1999).

The level of availability at which the threshold occurred was influenced by the nutritional quality of the high-quality food offered. Sheep started including wheat straw at higher levels of availability when alfalfa was used as a high-quality food instead of corn. Sheep showed similar intake rates for corn and alfalfa (0.40–0.49 g/s versus 0.44–0.59 g/s, 95% confidence limits; respectively); however, corn has greater energy content than alfalfa (13.2 versus 8.5 MJ/kg, respectively; National Research Council, 1985), which may allow a higher rate of energy intake. Therefore, if sheep in the present study were following a maximization of energy intake rate criterion (Van Wieren, 1996), an earlier inclusion of wheat straw in the diet when alfalfa is available in the foraging scenario instead of corn is expected.

The feeding environment in which sheep ate the wheat straw during the conditioning phase affected the experience they had with it. Although the mean intake of the wheat straw during conditioning was similar between treatment groups, sheep in CS+ showed a faster increase in wheat straw intake than sheep in CS- (see also Freidin et al., 2012, 2011). The effects of condition-

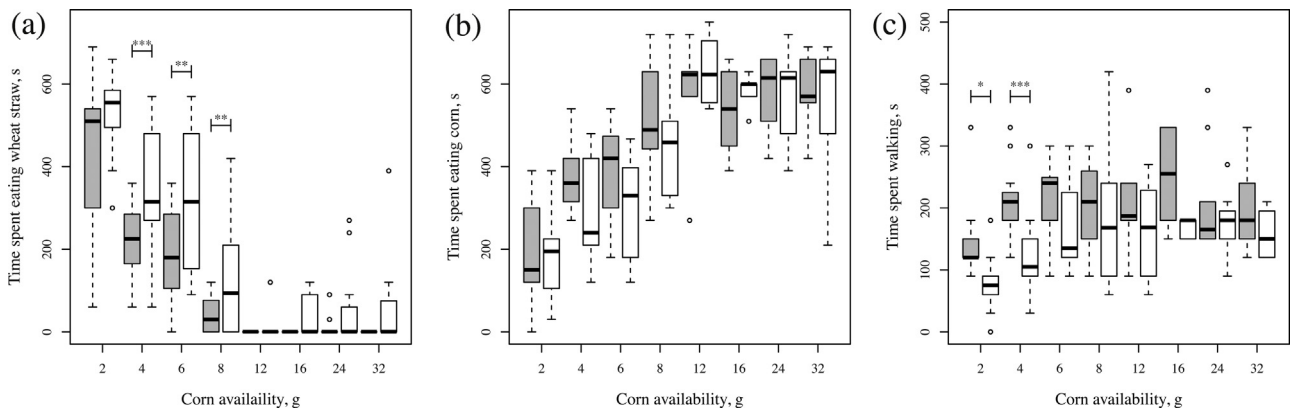


Fig. 4. Mean time spent eating wheat straw (a), mean time spent eating corn (b), and mean time spent walking (c) by individual sheep either previously exposed (CS+, white boxes) or not previously exposed (CS-, grey boxes) to a preference conditioning procedure during the last two sessions of testing in a foraging scenario in which the availability of corn in each feeding site was restricted to 2, 4, 6, 8, 12, 16, 24, or 32 g per animal. Box plots show the median (black line), the interquartile range (box), the minimum and maximum values within 1.5 times the interquartile range of the box (whiskers) and outliers (circles). Comparisons between treatments at each level of availability were performed using Tukey's HSD test. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

ing are difficult to observe when food acceptance (i.e., intake of a single food) is taken as response variable, probably because acceptance is affected by hunger (in this study, sheep were fasted for 16 h) (Sclafani, 1997). However, the contrasting experience of sheep in CS+ and CS- with the wheat straw during conditioning was not consistently expressed over the whole range of availabilities of high-quality foods. Free-choice tests conventionally used in preference conditioning studies (e.g., Sclafani, 1997) have the implicit assumption that responses to a given stimulus during a choice should be proportional to its relative rewarding properties (“matching law;” Baum, 1974). If so, increases in the incentive value of a given food (e.g., following a conditioning procedure) should produce a proportional increase in the animal’s response towards this food, irrespective of the contextual situation provided by higher-quality alternatives. We observed that while feeding response to the high-quality food was linear and proportional to its availability in the foraging scenario (this can be explained by functional responses previously observed in herbivores; Spalinger and Hobbs, 1992), the sheep’s intake of wheat straw showed a non-linear response to the availability of the high-quality food, which also conditioned the expression of previous experience. When the availability of the high-quality food was high, both groups of sheep showed almost negligible and similar intakes of wheat straw, whereas when the availability of the high-quality food was low, striking differences in wheat straw intake between sheep in CS+ and CS- were revealed. In agreement with this result, Ralphs (2005) observed that sheep conditioned with glucose to ingest *Delphinium occidentale* (a toxic plant) showed a greater preference for the toxic plant than control sheep, but only when the preferred herbs in the plant community were almost depleted. Similarly, experienced sheep showed greater preference for the shrub *Artemisia tridentata* (high in secondary compounds) than inexperienced sheep, but only when animal density was increased and the probability of encountering preferred herbs declined over time (Shaw et al., 2006).

Learning models of diet selection and optimal foraging models provide seemingly independent explanations for the same phenomenon (Bailey et al., 1996; Provenza et al., 2003; Simpson et al., 2004). However, both models share complementary information about the environment and foraging decisions of herbivores. In the present study, previous experiences with the wheat straw impacted foraging strategies, but only when contextual information (i.e., availability of the high-quality foods) was manipulated. At first, this behaviour is consistent with an optimal use of information about food ranking, which assumes that the likelihood of a given food type to be included in the diet depends not only on its own profitability but also on the encounter rate with higher-ranking foods (Charnov, 1973). However, sheep in CS+ started including wheat straw into their diet at similar levels of availability of the high-quality food when compared to sheep in CS- (i.e., the level of high-quality food in which the inflection in behaviour was observed did not differ between groups). This contradicts the expected response when assuming that, as a consequence of previous conditioning, the wheat straw was valued as “higher-ranking” by sheep in CS+.

There is still debate about what is learned during the oral-delayed conditioning paradigm (Freidin et al., 2012, 2011). Traditional learning processes, as “post-ingestive feedback” mechanisms, may act differently from other alternative learning processes (e.g., those involved in the conditioning between foods of different nutritional value) during the development of food preferences. For instance, nutrient-specific preferences can be conditioned with intragastric infusions of nutrients (i.e., post-ingestive feedback learning; Villalba and Provenza, 1999), but this was not corroborated with oral-delayed conditioning procedures (Pérez et al., 1995). Learning can also affect different components of the incentive value of foods, such as “wanting” and/or “liking” (Berridge

et al., 2009), and therefore can have different impacts on the animal’s responses (see also Ginane et al., 2015). For instance, appetitive and consummatory responses to food and water are increased in hyperdopaminergic mutant mice without being reflected in increased “liking” reactions (Peciña et al., 2003; see also Myers and Sclafani, 2003). When sheep in CS+ showed greater intake of the wheat straw than sheep in CS-, this was not associated with higher intake rates, which may indicate that the motivation to eat the wheat straw was similar between groups (Nielsen, 1999). The increased wheat straw intake of sheep in CS+ is probably better explained by differences in foraging strategy, in which sheep in CS+ spent more time foraging the low-quality food and less time foraging the high-quality food than sheep in CS-, while sheep in CS- increased time spent searching (i.e., walking) for the preferred alternative.

Different behavioural and learning patterns have relevance at different levels of environmental heterogeneity, and this is how herbivores’ foraging scales can be defined functionally (Bailey et al., 1996). Based on our results, we suggest that foraging decisions at finer scales, in which animals decide between individual plants or plant parts, are not affected by previous context-dependent experiences with low-quality foods (i.e., rewarding properties may be independent of context-dependent experiences). Determination of food ranking and discrimination between alternative foods is most probably ruled by basic forms of learning; for instance, the post-ingestive feedback between the nutritional content and the external attributes of foods (Provenza, 1995). Instead, the possible associations between the properties of two different foods in the foraging environment (Yearsley et al., 2006), may affect decisions made at a higher hierarchy in the foraging scale, where food types are already chosen and animals have to decide how long to stay foraging before resuming searching (i.e., “giving up time” *sensu* Charnov, 1973). Similarly, European starlings (*Sturnus vulgaris*) have accurate knowledge of the rewarding properties of a given patch that is mostly independent of contextual manipulations; however, the time for moving on to a new patch was affected by contextual information (Kacelnik and Brunner, 2002).

The present study contributes to strengthen the hypothesis that information about food resources is gained by foraging experience and learning, which relaxes the assumption of “complete information” in traditional OFT model. We suggest that in nature herbivores’ experiences with low-quality foods vary as a function of the profitability of feeding on the higher-quality alternatives. For instance, low availability of high-quality foods should encourage herbivores to include lower quality options, and as a result, the simultaneous ingestion of these nutritionally contrasting foods may change the learned incentive value of low-quality foods. Villalba et al. (2004) observed that lambs previously offered restricted amounts of a high-quality food and alternative foods with toxins showed, in posterior trials, greater preference for the foods containing toxins than lambs offered unrestricted access to the high-quality food. Animals following a “Bayesian-like” (*sensu* McNamara et al., 2006) foraging decision-making have *a priori* information about a low-quality food probably linked to external cues (e.g., flavor, smell, texture, etc.) signaling its low nutritive or toxic properties; however, information can be updated through foraging experiences to form “posterior opinions,” in which contextual experiences are probably involved. The question that arises here is what is the biological or ecological significance of having this type of contextual valuation about low-quality foods? Sheep in CS+ showed lower intake of alfalfa (but not corn) than sheep in CS-, which may have reduced the total ingestion of nutrients (as observed in a previous study by Catanese et al., 2015). The use of context-dependent information can lead to an apparent “sub-optimal” decision-making (Freidin and Kacelnik, 2011). However, this type of information can be valuable for consumers if

we consider its profitability in terms of utility instead of absolute gains (Kacelnik and Marsh, 2002). Although the absolute nutritional value of the wheat straw was similar to both groups of sheep (i.e., CS+ and CS-), it is well known for ruminants that ingestion of a food resource with high content of structural carbohydrates like wheat straw paired with a source of protein improves digestion and thus nutrient yield (Church and Santos, 1981). Therefore, when the availability of high-quality foods in the environment is low, increased ingestion of low-quality foods stimulated by previous context-dependent experiences may lead to improved nutrient gains relative to the strategy of first depleting the high-quality food resources and then continuing with the inclusion of low-quality foods (see also Pompilio et al., 2006).

To summarise, sheep in both treatments gathered different information about the same low-quality food as a product of different past experiences with that food. The expression of previous learning was closely related to an optimal foraging use of information associated to the lower-quality food option in the foraging scenario. When availability of the high-quality food was low and it was probably optimal to start including the low-quality food into the diet, sheep with a previous positive experience with this food showed higher intake than sheep deprived from this experience. However, a past positive experience with the low-quality food did not increase the likelihood of this food being included in the diet at higher levels of availability of the high-quality food in the environment. Therefore, our implicit assumption that the low-quality food was valued as higher-ranking by sheep exposed to the preference conditioning protocol used in the present study was not supported. Caution should be taken when generalizing learning obtained during an oral-delayed conditioning procedure (as in the present study) to more basic forms of learning, such as the traditional post-ingestive feedback paradigm. We consider that the present study encourages further research to explore which aspects of the incentive value of foods (Berridge et al., 2009) are affected by the particular context in which the alimentary experience takes place, and how such context-dependent learning affects herbivores' decisions at different scales in the foraging process.

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