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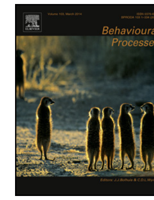

How the foraging decisions of a small ruminant are influenced by past feeding experiences with low-quality food

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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.

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).

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

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model of diet selection is that the incentive value of a low-quality food – and thus its preference – can increase trough 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 ± SD]) were kept as a group in a protected enclosure (20 × 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 × 6 m, length × 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 × 50 cm, length × width, and 20 cm high) at both ends. The buckets had two equal inner compartments (15 cm × 25 cm, length × 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.