Short report

Do grazing sheep use species-based categorization to select their diet?

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ABSTRACT

Food item categorization should reduce the cost of information processing by herbivores when selecting their diet in complex environments. We assessed the ability of sheep to categorize food items by offering them ryegrass (Rg) and fescue (Fe) in pots cut tall (T) or short (S). Ewes’ preferences were tested in three binary choices, RgS–FeT, RgS–FeS and FeT–FeS, before and after aversive conditioning against RgT. After conditioning, the ewes decreased their preference for RgS, but their choice between tall and short fescue was unchanged. Thus the ewes generalized their aversion to the species but not to the sward height. Comparing the choices between the two species offered at the same height showed choices were similar between RgS and FeS here and between RgT and FeT in Ginane and Dumont (2006). We conclude that sheep can use species-based, open-ended categorization when selecting their diet, while other plant characteristics, such as sward height, are not used to define a category, despite their importance in diet selection.

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1. Introduction

In semi-natural pastures, herbivores select their diet among many different plant items. They are thus faced with a multitude of stimuli when deciding what to eat and what to avoid. Little is known about the respective roles of deliberate selection and random processes when animals have to deal with such large amounts of information. Ability to assign food items to categories (Herrnstein, 1990) should considerably reduce cognitive demand (Zayan and Vauclair, 1998) and thereby increase the foraging efficiency of grazing herbivores. If animals were shown to use such a process, knowledge of the plant characteristics defining the categories would help to predict dietary choices in complex environments.

The few studies that have dealt with the ability of ruminants to generalize food preferences or aversions have shown that lambs can generalize food knowledge on a flavour basis (Launchbaugh and Provenza, 1994; Villalba and Provenza, 2000a,b). Ginane and Dumont (2006) have shown that ewe-lambs also generalize a conditioned aversion for tall ryegrass to short ryegrass but not to tall fescue. They could thus generalize to a species but not to a transient state like sward height.

Generalization and categorization are different processes. Generalization implies the assessment of similarity between stimuli and a graded response along a perceptual scale (Ghirlanda and Enquist, 2003). Categorization is an ability to group items on the basis of common features and respond similarly to them (Urcioli, 2001; Zentall et al., 2002). Generalization is required for categorization but not the reverse (Benard et al., 2006); hence categorization must make higher cognitive demand. Our earlier work did not allow any conclusion to be drawn concerning the categorizing ability of grazing sheep: this was the objective of the present study.

2. Materials and methods

The study was conducted indoors at the INRA-UR1213 experimental farm in France (45º 42’N, 03º 30’E) between August and early October 2006. The animals were handled by specialized personnel who applied animal care and welfare in accordance with European Union Directive No. 609/1986.

2.1. Animals, swards and test arena

We used nine Romane ewes aged 18 months (initial mean live weight: 55.4 kg, S.D. 8.11), chosen from an initial batch of 15 on the basis of their habituation to isolation in the test arena after a 10-day training period. Outside the tests, they grazed on cocksfoot with free access to water and salt blocks.

Experimental swards were ryegrass (Lolium perenne cv. Ohio) and fescue (Festuca arundinacea cv. Jordane) sown in pots (0.39 m × 0.315 m × 0.26 m), 232 and 237 in number, respectively. Both species were offered tall (12 cm) and short (6.5 cm), thus forming four different items: tall ryegrass (RgT), short ryegrass (RgS), tall fescue (FeT) and short fescue (FeS).

We used the same test arena composed of four pens as in Ginane and Dumont (2006). Animals were held in the waiting pen from 7:30 a.m. to 4:00 p.m., where they had free access to water but...
no food. Two crossing pens between the waiting and test pens were used to isolate the tested animal from its peers. The test pen (2.5 m × 1.8 m) had a rounded end so that six pots were simultaneously accessible for the ewe in only one or two steps.

2.2. Procedure

The trial consisted of four successive choice periods (P1–P4) and three interpolated aversive conditioning sessions. Choices never included RgT, the item against which the animals were adversely conditioned. Animals were thus offered one of the three following choices each day: RgS–FeS, RgS–FeT or FeT–FeS. Choice periods lasted 3 days. Tests were randomized across animals and days in each period. There were always six pots in each test session with three of each item. Their respective position was predetermined so that no more than two pots of the same item were adjacent. Animals were tested alone between 1:30 p.m. and 3:00 p.m., for 4 min 30 s (i.e. 270 s) from the first bite taken in a randomized order. An observer watched from a mezzanine overhanging the testing area to avoid disturbing the animal. Behavioural activities were encoded using The Observer™ software (version 5.0, Noldus, The Netherlands). Grazing durations for each pot allowed choices for the two items to be assessed as a proportion of total grazing time. We also used instantaneous intake rates measured by Prache and Damasceno (2006) on dry Romane ewes grazing both sward species within a range of sward heights, to estimate relative preferences as the proportion of total intake.

Aversive conditioning was applied once between each choice period, between 11:30 a.m. and 12:00 a.m. We used lithium chloride (LiCl) as the aversive agent, administered by oral gavage using gelatine capsules and a veterinary dosing gun. The dose was 70 mg/kg BW, which had been shown to elicit partial aversion in our experimental conditions (Ginane and Dumont, 2006). Aversive conditioning sessions were conducted in a separate location to prevent any association between the discomfort induced by LiCl and the test arena. Eighteen tall ryegrass pots were presented in an arena in which all the animals were allowed to graze simultaneously for no longer than 5 min to prevent depletion. Each ewe received a capsule containing half the dose of LiCl corresponding to its body weight. The procedure was then immediately repeated with a new batch of 18 tall ryegrass pots.

2.3. Statistical analyses

Statistical analyses were performed with non-parametric tests, as most of the data did not meet the conditions for parametric analysis. Analysed data were grazing time or intake on each item of a choice type and the choice ratio. To assess the period effect (i.e. dependent data) we used the Friedman test, a non-parametric alternative to the ANOVA procedure for repeated measurements. To assess whether a food item was preferred we used the Wilcoxon paired test, comparing actual choices (expressed in grazing time or intake) with equal preference (i.e. 0.5). Finally, we used the Mann–Whitney test to compare the choice between short ryegrass and short fescue with that between tall ryegrass and tall fescue in Ginane and Dumont (2006). All the analyses were performed using XLstat software (Addinsoft, version 7.5).

3. Results

When preferences were expressed as proportions of grazing time, the ewes preferred short ryegrass to short fescue (P1 and P2: \( p = 0.004; P3: p = 0.02; P4: p = 0.04 \)) and tall fescue to both short ryegrasses (P1: \( p = 0.03; P2: p = 0.01; P3: p = 0.04; P4: p = 0.004 \)) and short fescue (P1: \( p = 0.004; P2, P3 and P4: p = 0.01 \); Fig. 1). Transitivity in preference was satisfied in all the periods and was thus unaffected by successive aversive conditionings. The only difference resulting from the expression of preferences in proportion of intake was that short ryegrass was preferred over short fescue in P1 \( (p = 0.02) \), both species being then equally preferred \( (P2: p = 0.30; P3: p = 0.84; P4: p = 0.65; \text{Fig. 2}) \).

Successive conditioning, however, always reduced preference for short ryegrass whether it was expressed as a proportion of grazing time \( (\text{RgS–FeS: } p = 0.02; \text{RgS–FeT: } p = 0.01; \text{Fig. 3}) \) or intake \( (\text{RgS–FeS: } p = 0.01; \text{RgS–FeT: } p = 0.01) \). In both cases, this decrease was mainly a result of reduced time spent grazing (or intake of) RgS \( (\text{RgS–FeS: } p = 0.001; \text{RgS–FeT: } p = 0.02; \text{Figs. 1 and 2}) \). Choice of FeT over FeS averaged 0.95 of grazing time and 0.97 of total intake and was not affected by successive aversive conditioning against tall ryegrass \( (p = 0.09) \).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{image1}
\caption{Grazing times (in seconds, mean ± S.E.M.) for the two food items in the different choice types through experimental periods P1–P4. Black: short ryegrass (RgS). Dark grey: short fescue (FeS). Light grey: tall fescue (FeT). Total duration of the tests: 270 s. Aversive conditioning sessions took place before P2, P3 and P4.}
\end{figure}

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{image2}
\caption{Intakes (in grams DM, mean ± S.E.M.) for short ryegrass (RgS in black) and short fescue (FeS in dark grey) through experimental periods P1–P4. Intakes are derived from measured grazing times and estimated intake rates on both swards based on Prache and Damasceno (2006). Aversive conditioning sessions took place before P2, P3 and P4.}
\end{figure}

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{image3}
\caption{Choice for tall (RgT, solid lozenges) or short ryegrass (RgS, open squares) offered with tall (FeT) or short fescue (FeS) through experimental periods P1–P4.}
\end{figure}
Finally, comparing the choices between the two species offered at the same height showed that choices were similar between RgS and FeS in this experiment and between RgT and FeT in Ginane and Dumont (2006) (P1: p = 0.95; P2: p = 0.40; P3: p = 0.66; P4: p = 0.27; Fig. 3).

4. Discussion

After conditioning against tall ryegrass, ewes reduced their preference for short ryegrass but not for tall fescue. They thus generalized their aversion to a species but not to a sward height, confirming our previous observations (Ginane and Dumont, 2006). There then remained the question of whether the animals’ response resulted solely from a generalization process or whether it also involved categorization. Categorization is the ability to group items on the basis of common features and respond similarly to them (Urcioli, 2001; Zentall et al., 2002). If animals can categorize items by plant species, we would expect similar patterns in the choice of tall or short ryegrass against fescue after negative conditioning against tall ryegrass. Fig. 3 shows similar qualitative trends for tall and short ryegrass but marked quantitative differences. These differences are due to the strong influence of sward height on the diet preferences of grazing herbivores (Dumont, 1997). Indeed, if we compare the choices the animals made between the two species offered at the same height (RgT vs. FeT and RgS vs. FeS; Fig. 3), patterns expressed in grazing time were identical, pointing to a categorization process.

In addition, categorization implies discrimination between different items in the same class (Sloutsky, 2003), while generalization has been viewed as resulting from a failure to discriminate in the inverse hypothesis (Lashley and Wade, 1946; Yarczower and Bitterman, 1965). In this last hypothesis, subjects generalize to the extent they cannot discriminate (Honig and Urcioli, 1981). The ewes discriminated between tall and short swards of the same species, as shown by clear preferences for the tall alternative before conditioning (0.92 ± 0.03 of grazing time for fescue; 0.93 ± 0.04 for ryegrass in Ginane and Dumont, 2006). Therefore, the similar qualitative trends for tall and short ryegrass (Fig. 3) cannot be attributed to any lack of discrimination between these items.

Thus, we find that ewes use a species-based categorization process when selecting their diet. This is an open-ended categorization, as a new item (RgS) is correctly assigned to a predefined class (ryegrass) through a perceptual similarity (Herrnstein, 1990).

Finally, while sward height greatly influences the diet preferences of grazing sheep, the ewes did not transfer the acquired aversion against tall ryegrass to tall fescue, the choice between the two fescues being unaffected by aversive conditioning (Fig. 1). Hence not all the perceptual cues that are important in discrimination and diet selection are used by the animals to define categories. Our method reveals this pattern, as the animals were directly rewarded by consuming the food items, compared with classical procedures in which animals are shown pictures and equally rewarded for positive responses (Huber, 2001; Benard et al., 2006; Marsh and MacDonald, 2008). This may be because sward height is a transient state, unlike intrinsic plant characteristic such as species, which sheep categorize. This suggests that sheep do not consider food items as a whole but rather as a set of attributes, transient or intrinsic, that they process differently. It remains to be determined which other plant characteristics (e.g., botanical family) are used by herbivores to define categories in complex environments, and which are ignored.

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References


