Research Note

Learning Through Foraging Consequences: A Mechanism of Feeding Niche Separation in Sympatric Ruminants

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Abstract

Explanations for why sympatric ruminant species select diets composed of different plant species or plant parts have been controversial. Our explanation is based on learning from foraging consequences, which includes the influences that morphology, physiology, and experience have on diet selection. We conducted a trial with cattle (*Bos taurus*), sheep (*Ovis aries*), and goats (*Capra hircus*) and leafy spurge (LS; *Euphorbia esula* L.) to explore the interface between the learning and morphophysiological foraging models with these sympatric ruminants. After a pretrial adjustment period, the control group for each species received, via stomach tube on days 1 and 2, ground grass after eating a novel food (NF; rolled corn), and the treatment group for each species received ground air-dried LS after eating the NF. NF intake on days 2 and 3 was expressed as a percent of NF intake on day 1, and it declined considerably for cattle and sheep dosed with LS but did not decline for goats receiving it ($P = 0.001$). LS elicited learned aversive feeding responses from cattle and sheep but not from goats. The results are consistent with field observations that goats graze LS more readily than sheep or cattle do. Learning from foraging consequences offers an explanation for the unique diets of sympatric ruminant species.

Resumen

Las explicaciones sobre los diferentes tipos de plantas o partes de plantas en las dietas de rumiantes "simpátricos" son aun polémicas. Nuestra explicación esta basada en el aprendizaje de las consecuencias del forrajeo, que incluyen las influencias de la morfología, la fisiología, y la experiencia en la selección de la dieta. Realizamos un ensayo con ganado vacuno (*Bos taurus*), ovino (*Ovis aries*), y caprino (*Capra hircus*), y con la euforbia "leafy spurge" (*Euphorbia esula*) para explorar el interface entre aprendizaje y los modelos morfo-fisiológicos de forrajeo en estos rumiantes "simpatricos." Después de un período inicial de ajuste (pretratamiento), el grupo de control para cada especie recibió durante el primer y segundo día, vía tubo estomacal, "ground grass" después de comer "novel food" (NF; maíz rodado) y el grupo de tratamiento para cada especie recibió "ground air-dried LS" después de comer NF. La ingestión de NF en el segundo y tercer día se expresó como un porcentaje de NF en el primer día y se redujo considerablemente para vacunos y ovinos alimentados con LS, pero no se redujo para caprinos ($P = 0.001$). LS provocó respuestas adversas de alimentación aprendida por parte de vacunos y ovinos pero no de caprinos. Los resultados son consistentes con observaciones de campo en las cuales caprinos pastan LS con mas facilidad de ovinos y vacunos. El aprendizaje de las consecuencias de forrajeo ofrece una explicación sobre la particularidad de las dietas de especies de rumiantes "simpatricos."

Key Words: diet selection, herbivory, cattle, sheep, goats

INTRODUCTION

Partitioning of food resources by mammalian herbivores has been explained by differences in body size and/or digestive system morphophysiology (Schwartz and Ellis 1981; Hanley 1982; Demment and Van Soest 1985; Illius and Gordon 1987; Hofmann 1989; McArthur et al. 1991; Gordon 2003), species-specific specialization on grass growth stages (Murray and Brown 1993), and competitive vegetation modification (Murray and Illius 1996). Influence of plant defensive compounds on diet selection of mammalian herbivores is recognized (McArthur et al. 1991; Murray and Illius 1996; Duncan

and Gordon 1999), and it is known that interspecific differences exist among ruminants for tolerance and response to phytotoxins (Kronberg and Walker 1993; Cheeke 1994). However, interspecific differences in diet selection in response to phytochemical defenses has received little consideration as a basic factor influencing diet selection of sympatric mammalian herbivores.

Browsing and mixed feeding ruminants have larger livers relative to their body weight than grazers have (Hofmann 1989; McArthur et al. 1991) and may have greater capacity to detoxify phytochemicals. Forbs and browse generally contain more phytotoxins than do grasses. Why domestic and wild ruminants, which graze primarily grass and often consume only small amounts of forbs and/or browse (Van Dyne et al. 1980; Hansen et al. 1985), do not consume more of these plants since they are often abundant and nutritious is an important question. The ability to either detoxify phytochemicals in certain plants that are initially toxic or made toxic by rumen
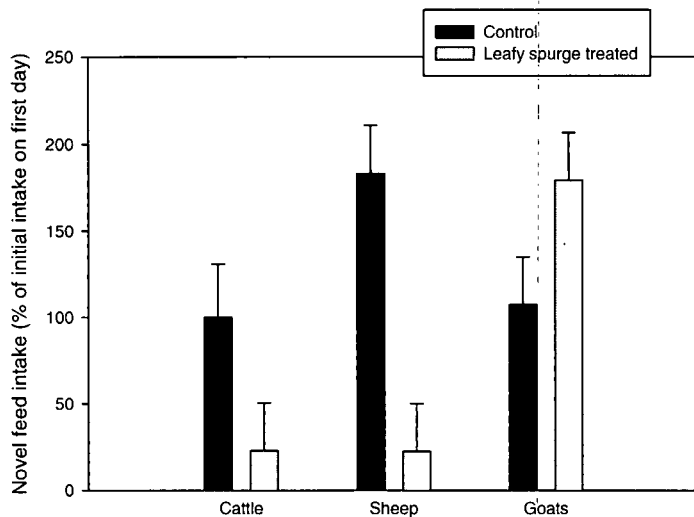
Figure 1. Novel feed consumption (% of initial intake of novel feed on first day of trial) by cattle, sheep, and goats receiving either crested wheatgrass (control) or leafy spurge after they consumed a novel feed. Bars represent standard error.

microbial metabolism (Kronberg et al. 2006) and consequently learn to ingest these plants or learn to avoid them if their toxicity cannot be minimized may be a primary but under appreciated factor differentiating diet selection among sympatric ruminants.

The objective of this study was to test the hypothesis that the learning through foraging consequences model (Provenza and Balph 1990) provides a plausible explanation for observed differences in diet selection by sympatric herbivores. Provenza and Balph (1990) acknowledged that their learning model and the alternative model based on morphophysiology are complementary and largely inseparable because learned behavior results from its consequences, and the consequences are determined by interactions among morphological and physiological processes. Our hypothesis was examined by testing whether the forb leafy spurge (LS; *Euphorbia esula* L.) induced learned feeding aversions in domestic cattle, sheep, and goats. Leafy spurge has high nutrient density (Fox et al. 1991) and is readily consumed by domestic goats (*Capra hircus*; Walker et al. 1994; Lym et al. 1997) and by domestic sheep (*Ovis aries*) in some but not all locations (Kronberg and Walker 1999) but is avoided by cattle (*Bos taurus*; Lym and Kirby 1987; Hein and Miller 1992) and some wild ruminants (Sullivan et al. 1988).

METHODS

Ten yearlings each of cattle, sheep, and goats were randomly divided into 2 groups per species ($n = 5$ per group) for the trial. Average body weights with standard deviations for the cattle, sheep, and goats were 244.6 ± 38.9, 53.4 ± 4.8, and 31.0 ± 5.5 kg, respectively. One week before the trial started, animals were fed a basal ration of alfalfa hay ad libitum for 12 h/d. During the weeklong pretrial period, animals were offered a small amount of barley (*Hordeum vulgare* L.) grain in individual outdoor pens from 0700 to 0730 hours to accustom the animals to the trial procedure. Hay was withheld for 12

hours before animals were offered barley grain. Following the pretrial period, a 3-day trial was conducted. For each species, a control group received ground crested wheatgrass (*Agropyron cristatum* L.) after eating a novel food (NF; rolled corn [*Zea mays indentata* L.]), while a treatment group received ground LS after eating the NF. Cattle, sheep, and goats were offered 1 kg, 300 g, or 300 g, respectively, of NF daily from 0700 to 0730 hours in individual outdoor pens. Both grass and LS were air-dried, ground, and dosed intraruminally with a stomach tube. Dosage rate of both plant materials was 0.15% of body weight, a reasonable amount of LS that these species could ingest in a morning grazing session. The ground material was mixed with just enough water to allow the slurry to pass down the tube, and similar amounts of water were used for grass and LS. Following dosing, they were released to large outdoor pens where alfalfa hay, water, and salt were available. Hay was withheld for 12 hours before animals were offered the NF. Animals received the treatments on trial days 1 and 2 and were tested for aversion to the NF on trial days 2 and 3.

To test for the effect of ruminant species and the food aversion treatment, NF consumption on days 2 and 3 were expressed as a percent of NF consumption on day 1 of the trial and will be referred to as $NF_{ti} \cdot NF_{t1}^{-1}$. This removed scale differences as a result of the different amount of NF presented to cattle compared to sheep and goats as well as reducing individual animal differences. The effect of NF as a covariate for $NF_{tx} \cdot NF_{t1}^{-1}$ was not significant ($P = 0.27$) and was not used in the final analysis. The final analysis tested for the effect of animal species (AS) and food aversion treatment (FAT) as fixed effects, day as a repeated random effect and all interactions. The General Linear Models procedure of SAS (1990) was used for the analysis. Individuals were nested within their treatment groups, and the mean squares for individuals within treatment were used as the error term to test for fixed treatment effects. Day was the subplot treatment. Day and the interaction of day with the fixed effects were tested with the residual mean square error. When appropriate, individual means were compared with the protected least significant difference (LSD) procedure.

All experimental procedures followed a protocol approved by the U.S. Sheep Experiment Station's Animal Care and Use Committee.

RESULTS AND DISCUSSION

Fixed effects and their interactions were significant ($P < 0.02$), but all random effects (i.e., day and interactions with fixed effects) were not ($P > 0.33$). Because day and its interactions were not significant but the AS × FAT interaction was ($P = 0.001$), only the interaction cell means for $NF_{ti} \cdot NF_{t1}^{-1}$ across replicate days are presented (Fig. 1). The interaction was caused by different responses to FAT by the ruminant species. Relative to this study, the most important effect was that pairing LS with a NF resulted in the formation of a learned food aversion in cattle and sheep but not goats. Treatment cattle and sheep consumed only 25% of their predosing level of NF compared to treatment goats, which increased their consumption of NF after being dosed with LS. Increased consumption of NF in control sheep indicates that initial intake was reduced by neophobia to the NF on day 1, which

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attenuated when its consumption was followed by positive feedback as a result of the high energy density in the NF.

Learned food aversion appears to explain why cattle and sheep consume less LS than goats do. Results are also consistent with our observations that sheep are reluctant grazers of LS in the area of Idaho where LS for the aversion trial was collected (Kronberg and Walker 1999). However, results are inconsistent with the general observation that sheep have a higher preference for LS than do cattle. Sheep may have the ability to adapt to LS ingestion over longer adaptation periods than what we used, or there possibly is a lower dosage of LS that causes learned food aversion in cattle but not in sheep. Kronberg et al. (1993) reported that LS induced a learned feed aversion in cattle that dissipated only slightly with 6 continuous days of LS introduction.

Given the observed gradient in intake of LS by grazing cattle, sheep, and goats with cattle generally eating little if any, goats preferring it, and sheep generally showing a neutral response to it (Walker et al. 1994; Kronberg and Walker 1999), we believe that one or more toxins in LS act to reduce ingestion of the plant to a greater degree in cattle and sheep.

Differences in diet selection from those predicted by morphological and physiological characteristics (e.g., Murray and Brown 1993; Sponheimer et al. 2003) can be explained by learning through foraging consequences. For example, cattle will readily graze the forbs *Medicago sativa* (L.) and *Melilotus officinalis* (L.) Pall. yet graze little if any LS. Interspecific differences among ruminants in respect to learned responses to a toxic plant that corresponds to observed interspecific differences in their grazing behavior has not, to our knowledge, been reported before.

Tolerance of phytotoxins by ruminants is determined largely by the rate in which they can be biotransformed in the animal. Important sites of biotransformation of phytotoxins include the rumen, gastrointestinal tract mucosa, liver, and kidney (Smith 1992; Cheeke 1994). Activities of liver, kidney, and gut enzymes that support biotransformation of toxins vary widely among domestic ruminant species (Smith et al. 1984; Watkins et al. 1986, 1987; Smith 1992), and transformation of toxins by rumen microbes also appears to vary among ruminant species (Wachenheim et al. 1992; Kronberg and Walker 1993). Ruminant species that lack capacity to minimize harm by phytotoxins will quickly learn to avoid or reduce their intake of a toxic plant to amounts they can tolerate (Cheeke 1994; Provenza 1995).

We conclude that the learning through foraging consequences model offers an explanation for differences in diet selection by sympatric ruminant species and agree that learning and morphophysiological models for diet selection are complementary and inseparable. Differential response to toxic and aversive phytochemicals among ruminants depends largely on differences in morphophysiology and experience. However, morphophysiological differences that influence food aversion learning (e.g., influence biotransformation of aversive compounds in the liver or other organs) are less obvious and more difficult to measure than morphophysiological differences such as body size, gastrointestinal tract dimensions, and incisor breadth.

Demment and Van Soest (1985) suggested that the evolution of the rumen was likely initiated by selection for detoxification or synthetic capabilities of foregut fermentation, and Duncan et al. (1990) postulated that the evolutionary success of ruminants may be a function of their ability to detoxify phytochemicals. We suggest that the differential capacity to metabolize toxic and aversive phytochemicals among ruminants in combination with their capacity for learning to avoid plants that induce aversive feedback are probably important components of food resource partitioning in sympatric herbivores. This concept is not addressed in the morphophysiological model, which is concerned primarily with the relationship of morphology and digestive physiology on the rate of nutrient capture (Illius and Gordon 1999). While rate of nutrient capture is important, our study shows that the ability of sympatric ruminant species to learn to decrease or increase intake of a particular plant is likely correlated with how their morphophysiology interacts with chemicals in the plant.

MANAGEMENT IMPLICATIONS

Improved understanding of why sympatric ruminant species differ in their ingestion and avoidance of plant species may help improve our ability to manage the interaction between rangeland vegetation and domestic or wild ruminant species.

ACKNOWLEDGMENTS

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