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Transmission of self-medicative behaviour from mother to offspring in sheep

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Herbivores challenged by diets with high concentrations of tannins learn by individual experience to self-select medicinal compounds such as polyethylene glycol (PEG), which neutralizes the negative postingestive effects of tannins. We investigated the transmission of this acquired self-medicative behaviour from mother to offspring. One group of ewes (experienced, $N = 8$) was conditioned to associate the beneficial effects of PEG after consuming a tannin-rich diet. Ewes ingested a meal of high-tannin food and were then offered PEG. Subsequently, ewes ingested the same tannin-rich meal and were then offered a food (grape pomace; control) that did not have the medicinal effects of PEG. After conditioning, the experienced group and a naïve group of ewes ($N = 8$) were given a choice between the high-tannin food, PEG and grape pomace. Experienced ewes showed higher intake and preference for PEG than did naïve ewes ($P < 0.05$). Subsequently, experienced and naïve ewes with their naïve lambs, as well as a group of naïve lambs without their mothers ($N = 8$), were exposed to the tannin-rich diet, PEG and grape pomace. Lambs were then tested for their ability to self-medicate with PEG by offering them a choice between the tannin-rich diet, PEG and grape pomace. Lambs from experienced and naïve mothers showed a higher preference for PEG than did lambs exposed without their mothers ($P = 0.05$). Thus, the presence of the mother (experienced or naïve) was important for naïve lambs to learn about the medicinal benefits of PEG. We conclude that the mother's presence per se may increase the efficiency of creating new knowledge, such as preference for a medicine, within a group, beyond transmitting and maintaining this knowledge across generations.

Social models play an important role in diet selection and food preferences of young animals (Thorhallsdottir et al. 1987; Galef 1991; Sclafani 1995). Socializing enhances learning efficiency because each animal no longer has to discover everything through trial and error (Thorhallsdottir et al. 1987; Provenza 1995; Provenza et al., in press) and this foraging information is passed transgenerationally from the experienced mother to the offspring (Key & MacIver 1980; Lynch et al. 1983; Green et al. 1984; Thorhallsdottir et al. 1990; Provenza & Cincotta 1993). A mother's influence on the diet of her offspring begins in utero (Nolte et al. 1992; Mennella et al. 2001), continues through the chemical composition and flavour of her milk (Nolte & Provenza 1991), and is particularly important as a young animal begins to forage prior to weaning (Chapple & Lynch 1986; Mirza & Provenza 1990, 1992, 1994; Thorhallsdottir et al. 1990).

While herbivores avoid toxic foods or prefer nutritious foods as a function of their mothers' avoidances or preferences (Mirza & Provenza 1990, 1992), no information is available regarding social transmission of other types of behaviours that are equally important for the fitness of the individual. Animals use plant secondary compounds and other non-nutritional substances to combat or control disease (Huffman 1997; Klein et al. 2008). Sheep self-select medicinal substances such as polyethylene glycol (PEG), a non-nutritive polymer that attenuates the aversive effects of tannins, and they increase intake of PEG as concentrations of tannins increase in the diet (Provenza et al. 2000; Villalba & Provenza 2001; Villalba et al. 2006).

In this study, we sought to determine the influence of the mother and the mother's level of experience with the medicinal effects of PEG after a tannin challenge on the transmission of self-medicative behaviour to her offspring. We predicted that (1) mothers trained to associate the beneficial effects of PEG while consuming tannins would transmit this information to their offspring, which would learn at a faster rate than the offspring of naïve mothers, and (2) lambs with social models would be more efficient at using PEG, even in the presence of a naïve social model, than would lambs without a social model.

METHODS

We conducted the study at the Green Canyon Ecology Center, Utah State University, Logan, UT, U.S.A. We housed 16 St Croix ewes

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(approximately 3–6 years of age) with their suckling lambs and eight St Croix lambs (approximately 2 months of age) in outdoor pens under a protective roof. Ewe–lamb pairs were penned in single, adjacent pens measuring 6 × 5 m, while the remaining eight lambs were penned in separate and adjacent individual pens (2.4 × 3.6 m). The animals were fed 1.5 kg of alfalfa pellets and 300 g of grain following daily trials. All animals had free access to sodium chloride with trace mineral blocks and fresh water throughout the study. Research protocols for the study were approved by an Institutional Animal Care and Use Committee (IACUC Approval 1409, Utah State University).

The ewes, each with their single lamb, were randomly assigned to a treatment group ($N = 8$ ewes and lambs) or a control group ($N = 8$ ewes and lambs). The third group included lambs without their mothers ($N = 8$ lambs).

The study was conducted in four phases. In the first phase, ewes from the treatment group were given experience to recognize the benefits of ingesting medicinal substances such as PEG when consuming a tannin-rich diet. In the second phase, we tested whether ewes from the treatment group learned about the benefits of PEG while consuming tannins by offering them choices between PEG and a nonmedicinal food (grape pomace). In the third phase, lambs with their mothers (experienced or inexperienced) or alone were offered a tannin-rich diet, PEG and grape pomace. After this exposure, we tested lambs' preference for PEG in a fourth phase.

Phase 1: Sequential Conditioning of Treatment Ewes

Conditioning with a medicine (PEG)

During conditioning with PEG, ewes from the treatment group were conditioned to experience the beneficial effects of PEG (medicine) at attenuating the postingestive stress caused by a diet high in tannins. Ewes were first fed a tannin-rich food and then offered PEG. Animals are more likely to learn about the benefits of a medicine when they experience illness and then ingest a medicine that leads to recovery (Provenza et al. 2000).

From day 1 to day 15 at 0845 hours, ewes were separated from their lambs with a panel that split the pen into two compartments. Lambs and ewes could still see, hear and smell each other. Thus, this sensory interaction added to the close proximity between mothers and their young, minimizing the negative effects of temporary separation (Price et al. 2003). Subsequently, ewes were offered a high-tannin diet (15% tannin (Tannin Corporation, Peabody, MA, U.S.A.), 55% alfalfa hay and 30% barley) from 0900 to 1000 hours and then offered PEG (MW, 3,350; Spectrum Chemical, Los Angeles, CA, U.S.A.) from 1000 to 1100 hours. Immediately after being offered PEG for 1 h, ewes were again offered the high-tannin diet for 1 h. After this procedure, each treatment ewe was reunited with her lamb and all animals were fed a basal diet of 1.5 kg alfalfa pellets mixed with 300 g barley.

Animals are initially reluctant to eat PEG, which has no nutritional value (Villalba & Provenza 2001). Hence, ewes were offered a 60:40 mixture of PEG:barley on day 1, with decreasing proportions of barley: 70:30 on day 2 and 80:20 on day 3. Thereafter, the proportion of barley was either increased or decreased based on the individual intake of each ewe in the group. If ewes ate more than 75 g of the PEG–barley mix, the proportion of barley was reduced to 10% for 1 day, and then eliminated (100% PEG) the next day. If ewes ate less than 75 g of the PEG–barley mix, the proportion of barley in the mix was maintained at 20%.

As the intake of PEG by ewes was low after 15 days of exposure, we increased the time of exposure to PEG. From day 16 to day 33, ewes were separated from their lambs and fed 1 kg of high-tannin diet from 0900 to 1000 hours, and were then offered 300 g of 100% PEG for 7 h. Refusals were collected at 1700 hours, the ewes were reunited with their lambs and all animals were fed the basal diet of 1.5 kg of alfalfa pellets mixed with 300 g of barley.

Conditioning with a nonmedicinal food (grape pomace)

In the conditioning phase with a nonmedicinal food, ewes from the treatment group were offered a low-quality feed (grape pomace) while experiencing the postingestive stress caused by a diet high in tannins. Treatment ewes were separated from their lambs, as described above, and fed 1 kg of high-tannin diet from 0900 to 1000 hours. Subsequently, we offered ewes 300 g of grape pomace (a novel food) mixed with 50 g of barley (a familiar food) to encourage them to sample the novel food. After day 8, the animals were fed 100% grape pomace. Refusals were collected and weighed at 1700 hours, the ewes were reunited with their lambs and all animals were fed the basal diet of 1.5 kg of alfalfa pellets mixed with 300 g of barley. Conditioning with grape pomace was conducted for 17 days until intake of grape pomace stabilized over time.

During phase 1, control ewes and their lambs were fed a basal diet of 1.5 kg of alfalfa pellets mixed with 300 g of barley.

Phase 2: Preference for PEG by Ewes

Ewes from the treatment and control groups were separated from their lambs, as described above, offered the high-tannin diet from 0900 to 1000 hours, and then offered a choice among the tannin-rich food, PEG and grape pomace until 1700 hours. Ewes were then reunited with their lambs. Refusals were collected and weighed, and the amount of medicinal/nonmedicinal food and tannin-rich diet consumed by the ewes was measured for 2 consecutive days.

Phase 3: Transmission of Self-medicative Behaviour

We conducted two consecutive trials, one of 7 days duration (period 1) and another of 5 days duration (period 2). Preference tests (see below) were conducted for all lambs after each period.

Ewe–lamb pairs and single lambs were offered a choice of the high-tannin food, PEG and grape pomace from 0900 to 1700 hours. Each ewe and her lamb ate together during this phase and, as opposed to single lambs without their mothers, daily intake of each food represented the combined consumption of the pair.

As an index for the ingestive behaviour of lambs and ewes during this phase, an observer recorded the foraging behaviour of each ewe and lamb at 5 min intervals from 0900 to 1030 hours (Altman 1974). We recorded incidences of feeding on each of the alternatives available as well as bouts of inactivity. Frequency of feeding on each alternative was calculated as a percentage of the total number of scans in which ewes and lambs were feeding. Total number of scans of eating events and noneating events (bouts of inactivity such as not eating or resting) was also recorded.

We collected and weighed refusals at 1700 hours and determined the intake of each feed at the end of each day. Ewe–lamb pairs received the basal diet of 1.5 kg of alfalfa pellets mixed with 300 g of barley; single lambs received 1 kg of alfalfa mixed with 300 g of barley.

Phase 4: Preference for PEG by Lambs

We determined lambs' preference for a medicine (PEG), a nonmedicinal food (grape pomace) and a tannin-rich food after exposure to these foods during phase 3. The day after each period of 'transmission of self-medicative behaviour', lambs were separated from their mothers, as described above, and offered a choice between the tannin-rich food, PEG and grape pomace from 0900 to