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Breed and maternal effects on the intake of tannin-rich browse by juvenile domestic goats (*Capra hircus*)

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ABSTRACT

Goat breeds differ in their consumption of tannin-rich browse, but the relative contributions of genetics and learning to these differences is unclear. The objective of this study was to differentiate between the effects of breed (nature) and rearing environment (nurture) on consumption of a tanniferous species by kid goats. We used Damascus and Mamber goat kids, and the browse species *Pistacia lentiscus* L. (tannin-rich) and *Phillyrea latifolia* L. (tannin-poor) to study the effects of breed and maternal attributes on: (i) propensity to consume these species when offered separately as a single food and (ii) preference when offered together. A cross-fostering experiment was conducted in which groups of Mamber and Damascus kids were reared indoors by biological mothers or by does of the reciprocal breed. To this design was added an artificially reared group of each breed that had been fed milk powder and had no adult role model. Propensity to consume and preference were tested prior to weaning when the "Naïve" kids had no foraging experience, and after the "Experienced" kids had been weaned and allowed to forage, either together with their treatment does or alone in the case of the artificially reared groups, in an area containing both target species. For both Naïve and Experienced kids, testing comprised nine 5-min exposures under controlled conditions. In the propensity test, Naïve and Experienced kids of all treatment groups consumed both browse species readily. In the preference test, the rearing doe had a significant effect on the preference for *P. lentiscus* shown by Experienced but not by Naïve, kids. This showed that that exposure to different role models while foraging induced differences in diet selection. Kid breed did not have a significant effect on preference for *P. lentiscus*. The preference for *P. lentiscus* shown by kids reared artificially (61%) or by Damascus does (55%) was significantly higher than that shown by kids reared by Mamber does (41%). This indicates avoidance learning rather than preference learning with respect to this plant species, and that kids may consume *P. lentiscus* readily in the absence of maternal influence. Learning appears to be far more dominant than genetics in determining goat kid preference/avoidance for tannin-rich browse.

1. Introduction

Diet selection by herbivores is influenced by a complex mix of intrinsic and external factors. Intrinsic factors include genetics (Ellis et al., 2005), health (Villalba et al., 2005), and hunger and other physiological feedbacks

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(Launchbaugh et al., 1999). External factors include plant availability (Murden and Risenhoover, 1993), plant toxicity (Provenza and Malechek, 1984), and social relations (Provenza and Burritt, 1991). In goats, diet selection is influenced prenatally in the mother's uterus (Nolte and Provenza, 1991) and subsequently, after birth, via milk consumption (Nolte et al., 1992) and by observation and imitation of maternal (Mirza and Provenza, 1990; Provenza et al., 1993) and peer (Thorhallsdottir et al., 1990) behaviour. Furthermore, the feeds an animal is exposed to early in life can also influence future diet selection (Ortega-Reyes and Provenza, 1992; Distel et al., 1994).

Plant secondary compounds that provide defense against herbivores form a major group of external factors that shape diet selection. Tannins constitute an important example of such compounds, which can drastically decrease palatability (Du Toit, 1990), feed intake (Barry and Duncan, 1984), nutrient (especially protein) availability (Makkar, 2003), and various enzymatic activities (Jones et al., 1994). At very high levels they can even be toxic (Bryant et al., 1991) and cause damage to the liver, kidneys, and the epithelium of the digestive tract (Reed, 1995).

Herbivores have developed physiological, anatomical and behavioural adaptations to help them cope with plant defense mechanisms (Makkar, 2003), and different adaptations have been found in different animal species (Squires, 1982), as well as in different breeds of a given species (Gall, 1981; Pritz et al., 1997; Walker et al., 2007). For example, Spanish and Angora goats in Texas differed in their ability to consume terpene-rich redberry juniper (*Juniperus pinchotii* Sudworth) (Pritz et al., 1997). In a Mediterranean shrubland, Damascus goats consumed more than twice as much tannin-rich *Pistacia lentiscus* L. (mastic tree) as did Mamber or Boer goats, despite the fact that there was an abundant supply of the palatable, low-tannin shrub *Phillyrea latifolia* L. (Glasser et al., 2006).

The relative contributions of genetics and learning to variations in diet composition are not well established. A better understanding of the relative importance of the roles of these intrinsic and external factors would indicate the extent to which they could be manipulated so as to change dietary preferences in order to achieve specific rangeland-management objectives, such as increased consumption of a target species. For example, in Mediterranean scrublands there is interest in using livestock grazing to control recent increases in woody vegetation cover that have lowered plant diversity and increased fire hazards (Perevolotsky and Seligman, 1998).

One approach to distinguishing between the effects of nature and those of nurture is by cross-fostering (Orr et al., 1995; Kruuk and Hadfield, 2007). We employed this approach in the present study, to quantify the effects of the rearing mother and breed on the intake of and preference for *P. lentiscus*, among Damascus and Mamber goats. The underlying rationale was as follows. If breed is the primary determinant of the observed behaviour, then kids of a given breed will behave similarly when reared by their natural mothers or by dams of the opposite breed. If learning is the primary determinant, then kids will behave according to whichever breed reared them. We extended the basic cross-fostering structure by adding a group that had been artificially reared, and which, therefore, would not exhibit any possible effect of learning from an adult. As a further means of teasing apart the various influences on diet-selection behaviour, we tested for any possible effect of the rearing treatments, both before animals were allowed to forage freely and to learn, and after they had the opportunity to learn from adults while foraging freely. During the latter rearing phase, all treatment groups had equal opportunities to gain free-ranging foraging experience (Provenza and Malechek, 1986) and familiarity with the foraging environment (Scott et al., 1996), in a 450-ha area. The specific objective of this study was to differentiate between the effects of breed (nature) and rearing environment (nurture) on the consumption of tannin-rich *P. lentiscus* by the kids.

2. Materials and methods

2.1. Study site

The study was conducted on the south side of the Mount Carmel ridge, Israel (32°25′ N, 34°52′ E), an area characterized by an average yearly rainfall of 600 mm and a 180-d rainy season from October to April. The ecosystem is a disturbed Mediterranean woodland (garrigue), characterized by rocky terrain with patches of shallow soil. The vegetation is dominated by low trees or tall shrubs (mainly *P. latifolia* L.) and moderate-sized shrubs (*P. lentiscus* L. and *Calicotome villosa* Poir. Link), which together form 2–3-m high coppices around islets that are sometimes covered with climbing *Rubia tenuifolia* D'Urv., *Clematis cirrhosa* L. and *Smilax aspera* L. Isolated common (*Quercus calliprinos*) and Tabor (*Quercus ithaburensis* Decne) oak trees, as well as carob (*Ceratonia siliqua* L.) trees and buckthorn (*Rhamnus lycioides* L.) shrubs can also be found. Occasional *Ephedra foemina* Forskk., *Asparagus stipularis* Forskk., and *Sarcopoterium spinosum* L. Spach bushes grow between the coppices. From January to mid-May, green annual herbaceous vegetation covers the soil patches (Glasser et al., 2008).

The tannin contents of *P. lentiscus* and *P. latifolia* are little affected by grazing or season (Perevolotsky and Haimov, 1991); they range from 15 to 25% and from 2 to 3.5%, respectively (Glasser et al., 2008).

2.2. Animals

The experiment was conducted with goats of the Damascus and Mamber breeds. The Damascus goat is common in Lebanon, Syria, Cyprus and Israel; mature females weigh about 55–60 kg, yield 300–600 l of milk in an 8-month lactation, and have an average prolificacy of 1.6 kids/litter. The Mamber goat is a small-framed animal, typical of the Middle East and is most common in extensive farming systems. It is a dual-purpose (milk and meat) breed, yielding approximately 120 l of milk per lactation, and has an average prolificacy of 1.1 kids/litter (Landau et al., 1995).

Twenty-six goats from each breed were estrus-synchronized prior to mating, in order to obtain the short kidding period necessary for successful fostering (Alexander et al., 1985). The goats were artificially inseminated with fresh semen collected from a buck of their own breed on 23 and 25 August 2005. After insemination, a buck of each breed was left with the females for natural mating.

Seventy-one percent of the goats gave birth in the period 12–27 January 2006. A further 14% kidded by 12 February, and the remainder kidded between 7 and 13 March. All the goats were kept indoors and stall-fed with alfalfa hay and concentrate feed (16% CP; Ambar feed mills, Hadera, Israel) from early January to early May 2006, to eliminate any possible effect of shrubland diet selection on milk composition or taste.

2.3. Animal treatments

The effects of the breeds of the kid and its rearing mother on consumption of and preference for *P. lentiscus* were investigated in a cross-fostering experiment, using the Damascus and Mamber breeds and three rearing environments in a full-factorial design. The kids were either reared by their natural mother, cross-fostered on the opposite breed, or reared artificially on milk replacer (artificial mother). Kids that were cross-fostered or artificially reared had been separated from their natural mothers immediately after birth. In the case of cross-fostering, kids from the two breeds that were born within 2 h of each other were smeared with reciprocal amniotic fluids and placed with their respective foster mothers.

In the following text, animal treatment will be specified with a capital letter for rearing mother (M: Mamber; D: Damascus; A: artificial) followed by a lower-case letter for breed of kid (m: Mamber; d: Damascus) (Table 1). There were a total of 50 kids in the experiment: nine kids in each treatment group with the exception of treatment M-d, which had only five kids because Mamber does were reluctant to adopt Damascus kids. Nevertheless, once adopted, there was no observable difference between this and any other treatment in the kid–dam bond. Kids of exceptionally high or low body weight (BW) were not used for the experiment. Each treatment group of kids was penned separately.

2.4. Experimental design

The effects of the six animal treatments were tested for both propensity and preference for *P. lentiscus* compared with those for *P. latifolia*. Propensity is the inclination or willingness to consume, as measured by intake rate, and this was determined by offering each browse species separately. Preference is the relative intake of a food that is offered together with other food items; it was determined by offering both browse species together. The propensity test was intended also to assist interpretation of the preference test: a strong preference for species B should be interpreted differently according to whether species A is consumed readily or only reluctantly when offered alone.

The propensity and preference tests were conducted at the end of each of two rearing phases. The first phase was prior to weaning, while the kids were housed, had only just started to eat dry feeds, and had not yet foraged freely; these kids were termed "naïve" at testing, which was conducted during 12–21 March 2006. The kids were then weaned and allowed to gain foraging experience in the shrubland area of the study site for the duration of the second rearing phase which lasted 4 weeks. During this experience phase each treatment group was kept separate and allowed to graze with their rearing mothers or, in the case of the Artificial rearing treatment, without any adults. Kids, now in the "experienced" state, were then tested during 4–15 June 2006.

Table 1
Animal treatments used in the experiments, and the number and mean weight (kg) of goat kids in each group weight class (L: light; M: medium; H: heavy), according to State.

Rearing mother	Kid breed	Abbreviation	Group weight class	Number of kids	State	
					Naïve (mean weight (kg))	Experienced (mean weight (kg))
Mamber	Mamber	M-m	L	3	13.2	22.2
			M	3	14.4	26.0
			H	3	14.8	28.0
	Damascus	M-d	M	3	12.3	27.6
			H	2	12.6	28.6
Damascus	Mamber	D-m	L	3	9.6	17.6
			M	3	10.4	21.0
			H	3	13.8	29.2
	Damascus	D-d	L	3	10.0	24.1
			M	3	10.3	24.6
			H	3	14.5	31.4
Artificial	Mamber	A-m	L	3	8.5	17.7
			M	3	12.7	21.7
			H	3	13.8	24.0
	Damascus	A-d	L	3	14.2	24.2
			M	3	15.0	27.2
			H	3	15.6	30.8

For each test state, i.e., at the end of each rearing phase, the nine kids of each treatment were stratified by live weight into a light, medium and heavy subgroup (replicate block), each of three kids. The kids of treatment M-d were divided only into medium ($n = 3$) and heavy ($n = 2$) subgroups. Average values for body weight are presented in Table 1.

Following stratification, the propensity to consume each target species was tested three times for each of the 17 subgroups, and the preference between the two species was tested three times for each subgroup. Every 2 days of propensity tests were followed by 1 day of preference testing. The sole purpose of performing the tests three times was to improve the propensity and preference estimates.

The order of the subgroups for each test day was determined by creating three random sequences of the six treatments, and randomly selecting a liveweight subgroup for each sequence–treatment combination (with one representing a dummy subgroup which was eventually ignored). For the propensity test, the two browse species were randomly allocated to the sequence–treatment combinations, with the constraint that each species appeared nine times each day and that each subgroup of animals was tested with each browse species three times in the course of the 6 days.

2.5. Experimental protocol

Separation of the treatment groups was maintained throughout the experimental period, both while they were housed and while they were gaining foraging experience. In the latter period, kids from each group grazed separately on the park premises for 4 h daily, and continued to receive a small concentrate supplement indoors.

The kids were exposed to the two browse species during the 14 days leading up to testing in the Naïve state; fresh branches were clipped daily and, in the afternoon, placed in a creep zone of each animal pen, in which only the kids could access the material. Residual material was removed the following morning. Nutritional composition of the plants is presented in Table 2.

The tests were conducted in a pen measuring 3 m × 3 m, surrounded by a bar fence and of similar construction to the treatment pens. In order to familiarize the kids with the test pen, during the first rearing phase they were able to leave the treatment pens by means of a creep mechanism, and to freely explore the test pen, where they had free access to concentrate feed.

For each test of a subgroup, several freshly cut branches of the one (propensity test) or two (preference test) target browse species were weighed and immediately stapled to a horizontal wooden plank that was fixed firmly at a height of 50 cm above the ground. The branches were presented so as to simulate, as far as possible, the morphology and resistance to pulling encountered under natural browse conditions, without any manipulation of the plant material. For the propensity test, average amounts (±SD) of 114 (±15) and 745 (±193) g, respectively, of browse were offered to subgroups of Naïve and Experienced animals. For the preference test, the positions of the two species along the plank were intermingled, and sufficient material of each species was presented to avoid depletion of either, even under strong preference. Subgroups of Naïve kids were offered 80 (±13) and 79 (±14) g of *P. lentiscus* and *P. latifolia*, respectively. Subgroups of Experienced kids were offered 542 (±66) and 497 (±88) g of *P. lentiscus* and *P. latifolia*, respectively.

For each species being tested, a reference branch was put aside to estimate evaporative loss during the test bout. The subgroup of kids to be tested was then introduced into the test pen and allowed to consume the browse for 5 min from the removal of the first bite by any kid. The kids were then returned to their treatment pen and the remaining plant material was removed from the plank and weighed. The reference material was then weighed a second time.

2.6. Statistical analysis

No corrections were made for moisture loss during the 5-min test periods, because the average weight loss from the reference branches during these periods was only 0.15% of their initial weight.

For the propensity test, the quantity (fresh weight) of browse consumed by a subgroup of kids during a 5-min test period was divided by the number of kids in the subgroup (which was three for all but one of the 17 subgroups) and expressed per unit metabolic weight (using an exponent of 0.75), where the metabolic weight was the mean metabolic weight of the animals in the subgroup. The average intake per unit metabolic weight for a subgroup was averaged over the three repetitions conducted within each test state (Naïve or Experienced). These averages were subjected to a full factorial analysis of variance (ANOVA) model with the JMP (version 7.0) statistical analysis software (SAS Institute Inc., Raleigh, NC). Terms in the model were: Kid breed (Damascus, Mamber); Rearing mother (Damascus, Mamber, Artificial); Browse species (*P. lentiscus*, *P. latifolia*); State (Naïve, Experienced); the six two-way and four three-way interactions among these terms; and group body weight class (Low, Medium, High). Three-way interactions among the main effects were examined, found to be not significant, and were excluded from the model. Similarly, non-significant two-way interactions were sequentially eliminated from the model, with the term with the

Table 2
Nutritional composition of the browse species *Pistacia lentiscus* L. and *Phillyrea latifolia* L. used in the two rearing phases (Naïve and Experienced) of the experiment. Polyethylene-glycol binding tannins (PEG-bT), Crude protein (CP), Neutral and Acid Detergent Fibre (NDF, ADF), and *in vitro* dry matter digestibility (IVDMD) are expressed in percentages, on a dry matter basis.

	n	Tannins		CP		NDF		ADF		IVDMD	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Naïve											
P. lentiscus	5	19.5	1.3	8.2	0.2	36.4	1.6	27.1	1.7	36.8	2.9
P. latifolia	5	1.4	0.6	8.5	0.6	44.5	3.5	28.9	2.9	49.6	1.9
Experienced											
P. lentiscus	9	20.7	1.4	8.3	0.3	37.9	1.4	28.0	1.2	38.1	1.2
P. latifolia	9	2.0	0.7	9.3	1.5	40.9	2.7	29.4	1.7	50.2	1.8

smallest F value being excluded at each step. Three two-way interactions remained in the final model, which had 55 error degrees of freedom. These two-way interactions were subjected to further ANOVA with the SLICE command which, for each level of one factor in the interaction, makes comparisons among all the levels of the other factor in the interaction.

For the preference test, data for the total browse consumption, as well as the quantity of each species consumed, were processed the same way as described above for the propensity test. In addition, following arcsine-root transformation, the fraction of *P. lentiscus* in browse consumed by a subgroup was averaged over the three repetitions conducted within each test state (Naïve or Experienced). These four dependent variables were subjected to a full-factorial ANOVA model. Terms in the model were: Kid breed (Damascus or Mamber); Rearing mother (Damascus, Mamber or Artificial); State (Naïve, Experienced); the three two-way interactions among them; and Group body weight class (Low, Medium, High). The model had 20 error degrees of freedom.

3. Results

3.1. Propensity test

The kids consumed both forage species willingly, as determined by direct visual observation. The factor State was highly significant in the analysis of consumption of both shrub species (Table 3): mean consumption increased from 1.82 g/(kg BW)$^{0.75}$ for the Naïve state to 3.27 g/(kg BW)$^{0.75}$ for the Experienced state. There were no significant main effects of kid breed, rearing mother or browse species on consumption, but there were significant interactions among these factors (Table 3).

Firstly, in the Naïve state, kids of all six treatment groups consumed more *P. latifolia* than *P. lentiscus* (2.01 and 1.63 g/(kg BW)$^{0.75}$, respectively; $P = 0.051$). In contrast, in the Experienced state, there was no consistent ranking of the consumption of the browse species across the treatment groups (3.10 vs. 3.45 g/(kg BW)$^{0.75}$ for *P. latifolia* and *P. lentiscus*, respectively; $P = 0.10$). These differences in browse consumption between the states resulted in a significant ($P = 0.016$) Browse species × State interaction.

Secondly, in the Naïve state, Damascus and Mamber kids consumed similar amounts of browse (1.72 and 1.92 g/(kg BW)$^{0.75}$, respectively; $P = 0.35$), whereas in the Experienced state, Damascus kids consumed more browse than Mamber kids (3.54 and 3.01 g/(kg BW)$^{0.75}$, respectively; $P = 0.015$). These differences in browse consumption between the kid breeds resulted in a significant ($P = 0.016$) Kid breed × State interaction.

Thirdly, if the kid breed was Mamber, then there was a significant ($P = 0.0027$) effect of Rearing mother on browse consumption, and natural rearing (i.e., Mamber kid reared by its own mother) resulted in the lowest consumption. No significant effect of Rearing mother on browse consumption was found for the Damascus kids. If the Rearing mother was Mamber, then Damascus kids consumed significantly ($P = 0.0033$) more browse than Mamber kids. Consumption of browse was similar between the Kid breeds for the Damascus and Artificial Rearing mothers. Consequently, there was a significant ($P = 0.0066$) Kid breed × Rearing mother interaction.

Table 3
ANOVA results of propensity test, following manual sequential backward elimination of non-significant two- and three-way interactions.

Source of variation	DF	F ratio	Prob > F
Kid breed	1	1.25	0.2693
Rearing mother	2	2.69	0.0768
Browse species	1	0.01	0.9236
State	1	99.38	<0.0001
Kid breed × Rearing mother	2	5.50	0.0066
Kid breed × State	1	6.16	0.0162
Browse species × State	1	6.16	0.0161
Group weight class	2	1.69	0.1938

3.2. Preference test

Total browse intake per unit metabolic weight was influenced primarily by State ($P < 0.0001$; Table 4); Experienced kids consumed more than twice as much browse as Naïve kids (4.37 vs. 2.02 g/(kg BW)$^{0.75}$). The effect of Rearing mother ($P = 0.073$) on total browse intake ranked Artificial (3.55) > Damascus (3.14) > Mamber (2.92 g/(kg BW)$^{0.75}$).

Intake of *P. lentiscus* per unit metabolic weight (Table 4) was influenced by State ($P < 0.0001$) and Rearing mother ($P = 0.0073$), and there was a significant Rearing mother × State interaction ($P = 0.024$). Kids raised by Mamber does (M-m and M-d) consumed significantly less *P. lentiscus* than kids raised by Artificial and Damascus does (A-d, A-m, D-d, D-m), with no difference between the latter (1.18, 1.77, 1.71 g/(kg BW)$^{0.75}$ for Mamber, Artificial and Damascus does, respectively). It is noteworthy that, in contrast to tannin-rich *P. lentiscus*, the intake of *P. latifolia* was affected

Table 4
ANOVA results of preference test.

Source of variation	DF	Total intake		*P. lentiscus* intake		*P. latifolia* intake		%*P. lentiscus* in diet	
		F ratio	Prob > F	F ratio	Prob > F	F ratio	Prob > F	F ratio	Prob > F
Kid breed	1	0.84	0.3689	0.005	0.9428	1.12	0.3011	0.48	0.4946
Rearing mother	2	2.9	0.0730	6.20	0.0073	1.57	0.2294	3.39	0.0518
State	1	118.6	<0.0001	101.5	<0.0001	25.92	<0.0001	8.22	0.0089
Kid breed × Rearing mother	2	0.92	0.4097	0.005	0.9950	1.26	0.3011	1.56	0.2323
Kid breed × State	1	0.94	0.3421	0.96	0.3358	0.15	0.6988	0.05	0.8169
Rearing mother × State	2	0.44	0.6444	4.46	0.0236	1.20	0.3184	3.06	0.0670
Group weight class	2	0.41	0.6648	0.53	0.5917	0.07	0.9313	0.04	0.9592

solely by State; the effect of Rearing mother was not important ($P = 0.23$; Table 4).

The percentage of *P. lentiscus* in consumed browse was influenced by State (41 and 52% for Naïve and Experienced, respectively; $P = 0.0089$; Table 4) and by Rearing mother (51, 48 and 41% for kids raised by Damascus, Artificial, and Mamber mothers, respectively; $P = 0.052$). There was no influence of Rearing mother on the Naïve state whereas there was a large effect ($P = 0.0062$) on Experienced kids, among whom *P. lentiscus* constituted 61, 55 and 41% of the browse consumed by kids raised by Damascus, Artificial, and Mamber mothers, respectively. This differential response probably accounts for the State $\times$ Rearing mother interaction ($P = 0.067$; Fig. 1).

4. Discussion

The propensity test enabled us to evaluate factors influencing the consumption of each plant species, in the absence of choice. Importantly, this test indicated no overall difference between breeds in their propensity to consume the respective browse species. Furthermore, in the transition from the Naïve to the Experienced state, no intake rate advantage to *P. latifolia* was evident.

In terms of the relative importance of genetics and learning, separate analysis of the propensity test for each browse species indicated a role for each of these factors in the case of *P. lentiscus*. The role of learning was evident in the fact that the intake rate of Mamber kids was influenced by their rearing mother, being lowest among the naturally reared kids. The role of genetics was evident in the finding that Damascus kids consumed more than Mamber kids when the rearing mother was a Mamber.

The preference test suggested that the influence of learning on diet selection was much stronger than that of genetics. In this test, kid breed had no influence on absolute intake or preference, whereas rearing mother did. Furthermore, the influence of rearing mother was apparent in the Experienced but not in the Naive state, a finding that

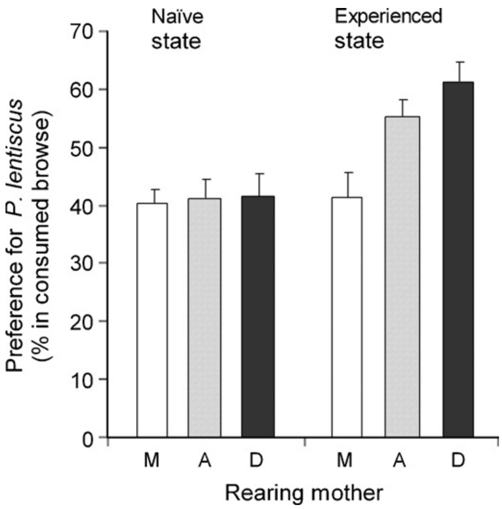

Fig. 1. Effect of State and Rearing mother on percentage of *P. lentiscus* in kids' diets during the preference test (M: Mamber; A: Artificial; D: Damascus). Bars indicate one S.E. of the mean.

is also consistent with a learning effect, because the opportunity to learn presented itself when adults and kids foraged together on the rangeland.

The present finding that a Mamber adult depressed the kids' preference for *P. lentiscus* is consistent with the finding of Glasser et al. (2006) that adult Mamber goats consumed less *P. lentiscus* than adult Damascus goats. The present findings suggest that the breed difference observed between adults derived from a learning process that started when the animals were juveniles. Furthermore, it seems that Mamber adults educated kids to reduce their preference for *P. lentiscus* rather than that Damascus adults educated kids to increase their preference. We draw this inference because kids without adults to learn from, i.e., those that were artificially reared, exhibited similar preference to those reared by Damascus adults (55% vs. 61%, respectively; $P = 0.59$); this indicates that, in the absence of a maternal influence, kids may consume tannin-rich *P. lentiscus* readily. Nonetheless, the finding that the two animal treatments (of the six) that ranked highest in terms of preference for *P. lentiscus* in the Experienced state were for kids raised by Damascus mothers suggests preference learning in the positive direction. These findings regarding the percentage of *P. lentiscus* in consumed browse show a strong influence of the rearing mother on kid dietary preference. The development of this attribute during the period between the Naïve and Experienced states (Fig. 1) reinforces the finding that there is a strong dominance of maternal training over genetics in transferring foraging skills to kids.

Manipulation of the rearing environment in combination with the transition between Naïve and Experienced states indicated that there is considerable plasticity in important aspects of foraging behaviour. It remains to be seen whether such manipulation could have a long-term effect on goat foraging behaviour, and whether a relatively simple manipulation such as artificial rearing would be adequate to break an inter-generational cycle of learning. If so, this could have far-reaching implications for the use of goats as a practical tool for land management, brush control, and targeted grazing practices.

5. Conclusions

The findings presented here indicate a strong dominance of learning over breed in the preference among goat kids for a tannin-rich woody species. Furthermore, they indicated that it was primarily a reduction rather than an increase in preference that was acquired in the learning process. Specifically, Mamber does educated their natural or fostered kids to avoid *P. lentiscus*, whereas the presence of Damascus does as role models did little or nothing to boost preference for this species, compared to having no role model at all.

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References

Alexander, G., Stevens, D., Bradley, L.R., 1985. Fostering in sheep: facilitation by use of textile lamb coats. Appl. Anim. Behav. Sci. 14, 315–334.

Barry, T.N., Duncan, S.J., 1984. The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 1. Voluntary intake. Br. J. Nutr. 51, 485–491.

Bryant, J.P., Provenza, F.D., Pastor, J., Reichardt, P.B., Clausen, T.P., du Toit, J.T., 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. Ann. Rev. Ecol. Sys. 22, 431–446.

Distel, R.A., Villalba, J.J., Laborde, H.E., 1994. Effects of early experience on voluntary intake of low-quality roughage by sheep. J. Anim. Sci. 72, 1191–1195.

Du Toit, J.T., 1990. Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. Ecology 7, 149–154.

Ellis, C.R., Royce, E.J., Scott, C.B., Taylor, C.A., Walker, J.W., Waldron, D.F., 2005. Sire influence on juniper consumption by goats. Rangeland Ecol. Manage. 58, 324–328.

Gall, C., 1981. Goat Production. Academic Press, London.

Glasser, T.A., Landau, S.Y., Ungar, E.D., Perevolotsky. A., Muklada, H., Dvash, L., Kababya, D., 2006. Comparing foraging behavior of goats from different breeds. In: Proc. 14th Ann. Conf. Israel Range Sci. Assoc. Bet-Dagan, Israel, March 2006, pp. 1–6 (in Hebrew).

Glasser, T.A., Landau, S.Y., Ungar, E.D., Perevolotsky, A., Dvash, L., Muklada, H., Kababya, D., Walker, J.W., 2008. A fecal NIRS-aided methodology to determine goat dietary composition in a Mediterranean shrubland. J. Anim. Sci. 86, 1345–1356.

Jones, G.A., McAllister, T.A., Cheng, K.J., Muir, A.D., 1994. Effect of sainfoin (*Onobrychris viciifolia* Scop) condensed tannins on growth and proteolysis by four strains of rumen bacteria. Appl. Environ. Microbiol. 60, 1374–1378.

Kruuk, L.E.B., Hadfield, J.D., 2007. How to separate genetic and environmental causes of similarity between relatives. J. Evol. Biol. 20, 1890–1903.

Landau, S., Perevolotsky, A., Carasso, Y., Rattner, D., 1995. Goat husbandry and production systems in Israel. In: El Aich, A., Landau, S., Bourbouze, A., Rubino, R., Morand-Fehr, P. (Eds.), Goat Production Systems in the Mediterranean. Wageningen Press, The Netherlands, pp. 136–159.

Launchbaugh, K.L., Walker, J.W., Taylor, C.A., 1999. Foraging behavior: experience or inheritance? In: Launchbaugh, K.L., Sanders, K.D., Mosley, J.C. (Eds.), Grazing Behavior of Livestock and Wildlife. Idaho Agric. Exp. Sta. Bull. 70. Univ. of Idaho, Moscow, ID, pp. 28–35.

Makkar, H.P.S., 2003. Effects and fate of tannins in ruminant animals, adaptation to tannins, and strategies to overcome detrimental effect of feeding tannin-rich feeds: review. Small Rumin. Res. 49, 241–256.

Mirza, S.N., Provenza, F.D., 1990. Preference of the mother affects selection and avoidance of foods by lambs differing in age. Appl. Anim. Behav. Sci. 28, 255–263.

Murden, S.B., Risenhoover, K.L., 1993. Effects of habitat enrichment on patterns of diet selection. Ecol. Appl. 3, 497–505.

Nolte, D.L., Provenza, F.D., 1991. Food preferences in lambs after exposure to flavors in milk. Appl. Anim. Behav. Sci. 32, 381–389.

Nolte, D.L., Provenza, F.D., Callan, R., Panter, K.E., 1992. Garlic in the ovine fetal environment. Physiol. Behav. 52, 1091–1093.

Orr, R.J., Penning, P.D., Parsons, A.J., Newman, J.A., 1995. The role of learning and experience in the development of dietary choice by sheep and goats. Ann. Zootech. 44, 111 (Abstract).

Ortega-Reyes, L., Provenza, F.D., 1992. Amount of experience and age affect the development of foraging skills of goats browsing blackbrush (*Coleogyne ramosissima*). Appl. Anim. Behav. Sci. 36, 169–183.

Perevolotsky, A., Haimov, Y., 1991. Structural response of Mediterranean woodland species to disturbance—evidence of different defense strategies. Israel J. Bot. 40, 305–313.

Perevolotsky, A., Seligman, N., 1998. Role of grazing in Mediterranean rangeland ecosystems. BioScience 48, 1007–1017.

Pritz, R., Launchbaugh, K., Taylor, J.R., 1997. Effects of breed and dietary experience on juniper consumption by goats. J. Range Manage. 50, 600–606.

Provenza, F.D., Burritt, E.A., 1991. Socially induced diet preference ameliorates conditioned food aversion in lambs. Appl. Anim. Behav. Sci. 31, 229–236.

Provenza, F.D., Malechek, J.C., 1984. Diet selection by domestic goats in relation to backbrush twig chemistry. J. Appl. Ecol. 21, 831–841.

Provenza, F.D., Malechek, J.C., 1986. A comparison of food selection and foraging behavior in juvenile and adult goats. Appl. Anim. Behav. Sci. 16, 49–61.

Provenza, F.D., Lynch, J.J., Nolan, J.V., 1993. The relative importance of mother and toxicosis in the selection of foods by lambs. J. Chem. Ecol. 19, 313–323.

Reed, J.D., 1995. Nutritional toxicology of tannins and related polyphenols in forage legumes. J. Anim. Sci. 73, 1516–1528.

Scott, C.B., Banner, R.E., Provenza, F.D., 1996. Observations of sheep foraging in familiar and unfamiliar environments: familiarity with the environment influences diet selection. Appl. Anim. Behav. Sci. 49, 165–171.

Squires, V.R., 1982. Dietary overlap between sheep, cattle, and goats when grazing in common. J. Range Manage. 35, 116–119.

Thorhallsdottir, A.G., Provenza, F.D., Balf, D.F., 1990. Ability of lambs to learn about novel foods while observing or participating with social models. Appl. Anim. Behav. Sci. 25, 25–33.

Villalba, J.J., Provenza, F.D., Shaw, R., 2005. Sheep self-medicate when challenged with illness-inducing foods. Anim. Behav. 71, 1131–1139.

Walker, J.W., Campbell, E.S., Lupton, C.J., Taylor, C.A., Waldron, D.F., Landau, S.Y., 2007. Contribution of breed, sex, and age to variation and predictive ability of near-infrared reflectance spectra of goat feces. J. Anim. Sci. 85, 518–526.