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Importance of Early Experience with Flavor on Subsequent Food Preferences by Young Coyotes (*Canis latrans*)

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ABSTRACT: Coyote food habits are well documented, but little is known about the mechanisms driving food selection. Early experience with flavors has been documented to be important in the foraging decisions made by such species as cattle, goats, rats, mice, and domestic dogs. We examined the effect of early experience with flavors on the subsequent food preferences of young coyotes. Part 1 of the study examined the effects of flavors presented in milk, while Part 2 examined the effects of flavors presented in solid food. In both parts, coyote pups were exposed to the treatments and subsequently tested with a series of two-choice tests. Results of the study indicate that early experience with flavor is not the sole mechanism driving food selection in young coyotes. These data support the hypothesis that young coyotes feed opportunistically.

KEY WORDS: behavior, coyote, *Canis latrans*, diet selection, early experience, food preference

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INTRODUCTION

Coyotes are generalist omnivores, consuming a variety of dietary items (Andelt, et al. 1987, MacCracken and Uresk 1984, Nowak and Paradiso 1983). Coyote food habits have been well documented, but very little is known about the mechanisms driving food selection.

Although the selection of certain dietary items is at least partially controlled by genetics, most choices are based on experience. Experience during all life stages (i.e., *in utero*, as a neonate, at weaning, as a juvenile, or as an adult) are important in helping an animal decide where and how to select a diet. A fetus' diet selection experience is limited to *in utero* exposure. After parturition, however, the neonate draws upon *in utero* experiences as well as those obtained while nursing. As the individual ages, its knowledge base develops through diet selection experiences. Experiences *in utero*, as a neonate, or during weaning could have profound effects on the adult animal's foraging decisions.

Although early experience with foods can increase the likelihood that those foods will be accepted later in life, studies have shown that over exposure to one flavor can cause aversion to that flavor resulting in different dietary preferences (Provenza 1996). Pregnant heifers fed only one flavor (i.e., coconut or maple) of ammoniated straw chose the alternate flavor during subsequent choice tests, presumably due to flavor satiation (Atwood et al. 2001). Rats given a 4-course meal ate less when all of the foods were flavored the same than when the foods were flavored differently (Treit et al. 1983). Additionally, rats given high energy foods in a variety of flavors consumed more and gained more weight than those given a diet containing only one flavor (Naim et al. 1986). Lambs fed apple- or maple-flavored food for one day preferred the same food in the alternate flavor the next day. The higher the energy content of the food offered, the greater the change in preference (Early and Provenza 1998). Therefore, any flavor eaten to satiety may cause a slight aversion resulting in the selection of varied dietary items. This change in preference probably occurs without any cognitive association on the part of the foraging animal; preferences can be altered even when an animal is anesthetized (Provenza et al. 1994), or tranquilized (Forthman Quick 1984).

Ferrell (1984) found that early exposure (i.e., one week *in utero*, in milk until weaning, and first-fed solid food at weaning) to cues reflecting the mother's diet influenced choices made by beagle pups during weaning. Seven out of 8 litters tested chose novel- over familiar-flavored foods. In the one instance where a litter strongly preferred the familiar flavor, it was more palatable than the alternative choice. It appears that repeated exposure to one flavor can cause flavor-satiety in domestic dogs, causing animals to choose a novel flavor.

Research suggests that adult coyotes are able to recognize particular flavors and can rank them in a preferential order. Coyotes placed a higher hedonic value on some tastes and preferentially consumed the valued tastes (Mason and McConnell 1997), and they associated flavors or taste with negative post-ingestive consequences (Ellins and Martin 1981, Gustavson et al. 1974). However, the role of learning in coyote pups on their subsequent food habits has yet to be elucidated.

EXPERIMENT 1

Our first objective was to determine whether experience with flavor in milk affected the diet selection behavior of young captive coyotes consuming solid food. Familiarity with a flavor may be an important factor in the diet selection of many wild animals (Shumake 1977). During weaning, rat pups preferentially consumed a diet with the same gustatory cues as that which was eaten by their lactating mother (Galef and Clark 1972, Galef and Henderson 1972, Galef and Sherry 1973). Similarly, Capretta and Rawls (1974) showed that rat pups exposed to garlic in mother's milk had a higher preference for garlic than those not previously exposed. Additionally, mice exposed to fennel in mother's milk ate more of a fennel diet than naive animals (Mainardi et al. 1989), and piglets consumed more of a weaning diet when it was flavored with the same compound sows received during lactation (Madsen 1977).

Methods

Subjects

Nine litters (49 individuals) of hand-reared coyote pups were obtained from breeding pairs at the United States Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS), Wildlife Services (WS), National Wildlife Research Center (NWRC) Logan, Utah Field Station. The pups were housed in kennels during testing and all trials were conducted during the late morning. Basal rations were made available each day.

Hand-Rearing Procedure

Pups were whelped in breeding pens with minimal human disturbance. All pups had adequate exposure to colostrum gained from nursing mothers' milk. At 10 days of age, pups were removed from their parents and brought to the nursery. Weights and temperatures were measured and the physical health of the pups was assessed by a veterinarian. All pups were marked to ensure that they could be individually recognized by the caretakers.

Coyote pups were hand-reared on canine milk replacer (PetAg, Inc., Hampshite, IL) and litters were randomly assigned to two treatment groups (milk replacer flavored with anise oil, milk replacer flavored with cilantro oil) or a control group (plain milk replacer). Flavors (Agrimerica-Lucta, Northbrook, IL) were chosen because they had distinctive tastes and were lipophilic. Additionally, a pilot study determined that the selected concentration (0.95%) of these flavors was adequate for adult coyotes to distinguish between the flavors on solid food, and that neither flavor was strongly preferred nor avoided. Exposure to test flavors began at the first bottle feeding attempt, and the amount of flavor in the milk remained constant throughout rearing.

Pups were fed using nursing bottles and nipples for human infants, and separate feeding paraphernalia was used for each treatment group to ensure that no cross-contamination occurred. Control litters were always fed first. Pups were fed 13 ml of milk replacer per 100 g of body weight during the first week of bottle feeding (Lewis et al. 1987). Total milk intake was spread across 5 daily feedings to yield approximately 8-12 ml of milk intake at each feeding during the first week. As the pups aged, the amount of milk fed at each feeding increased gradually with the body weight of the pup (up to 22 ml of milk replacer per 100 g of body weight). Pups were fed individually to ensure that each member of the litter received the proper amount of the correctly flavored milk replacer. Feeding of all pups within a litter was completed before feeding of the next litter was initiated. The amount of milk intake was strictly monitored to prevent overeating, which can cause gastric distress in young coyotes. If pups had difficulty suckling or refused to voluntarily eat, they were fed rations by oralgastric intubation, and electrolytes or 0.9% NaCl were administered when deemed necessary by a veterinarian.

Powdered milk replacer was mixed at the last feeding of the day for the next day's feedings. Flavoring was added to the milk at the time of mixing. All food preparation occurred in a location separate from the pup nursery to minimize contamination and exposure to the odor of the flavor additives. Flavored milk was stored in a refrigerator until used, but not for more than 24 hrs. Weaning began after the fifth week of bottle feeding. Pups were weaned to a commercially available kibble (Mazuri® Exotic Canine Ration, Richmond, IN).

Testing Procedure

Choice tests are most commonly used to evaluate food acceptances or preferences (Nolte and Mason 1998). In a two-choice test, an animal is presented with two options and consumption is measured after a predetermined period of time. Results of the two-choice test are often expressed as preference ratios between the choices offered (Ferrell 1984, Nolte and Mason 1998). A preference ratio of 0.5 indicates indifference for the item in the numerator, whereas a score of 0.0 or 1.0 indicates complete rejection or acceptance, respectively.

Preference tests were conducted at 3, 6, and 9 months of age. All pups were offered the choice between 100 g each of anise- and cilantro-flavored food and were given 45 seconds to consume the test foods. The diets were flavored by placing 4 ml of oil-based flavoring directly onto the kibble and mixing until evenly coated. Test food was weighed before and after the two-bowl test, and the gravimetric difference was used to calculate consumption. Trials were conducted once per animal for 4 consecutive days, and the total intake of each food was used to calculate a preference ratio for each animal. Each morning of the trial, all pups were given a basal ration of their maintenance diet equal to one-half their recommended daily allowance. The basal ration was given so diet selection would be driven by preferences rather than satiation. Trials were conducted 3 hrs after the consumption of the basal ration because moderately food-deprived animals provide more consistent results in two-choice tests (Nolte and Mason 1998). The location of the flavors (i.e., placed on the left or right) was counterbalanced to control for possible side preference of the animals (Ferrell 1984, Nolte and Mason 1998).

Preference ratios for the treatment animals were expressed as the amount of rearing-flavored food consumed divided by the total food consumed during the 4-day period. The control pups, however, were not reared on flavored milk. Therefore, we arbitrarily chose to express their preference ratios as the amount of cilantro-flavored food consumed divided by the total food (cilantro- and anise-flavored food) consumed during the 4-day period.

Given that litters of pups were randomly assigned to treatment, the individual preference ratios of the pups in a litter were averaged to determine a preference ratio for the entire litter. In this way, the preference ratio of each pup within the litter had equal weight in the determination of the mean preference score for the litter.

Preference tests also were conducted to determine if the flavor of the rearing diet was more preferred than that of an unflavored diet. All pups were offered the choice between unflavored kibble and kibble coated with the rearing flavor. Control pups were split into two groups, one receiving anise-flavored kibble during two-choice tests and the other receiving cilantro-flavored kibble. Two-choice tests were conducted as described previously. For the control pups, however, preference ratios were expressed as the amount of unflavored kibble consumed divided by the total amount of food consumed during the 4-day period. For these pups, ratios of 1.0 indicated a complete acceptance of the unflavored diet, and those of 0.0 indicated a complete acceptance of the offered flavored food. Individual animal preference ratios were averaged to determine a preference ratio for the entire litter.

Statistical Design

A mixed model repeated measures ANOVA was used to analyze the preference test data when testing the rearing flavor against the alternate diet (i.e., either the alternate-flavored rearing diet or the unflavored diet). In trials testing the rearing diet against that containing the alternate flavor, the ANOVA had 3 treatments (i.e., exposure to anise flavor, cilantro flavor, or no flavor in milk) with a variable number of replicates in each treatment. For trials testing the rearing diet against the unflavored diet, the ANOVA had 4 treatments because control pups were separated for the analysis based on the flavors received during trials. The experimental unit for this analysis was the litter with individual pups within the litter treated as subsamples. For both analyses, a value termed RATIODIF was used rather than the calculated preference ratios. RATIODIF was equal to each preference ratio minus the no-preference value (i.e., 0.50) as a constant. The intercept, least squares means, and confidence interval options were used to determine which, if any, of the ratio means were different than a no-preference value of 0.50. These options were reliant on RATIODIF to be effective. In all cases, the upper and lower bounds around each mean were determined. In all tests, mean preferences were considered different when $p > 0.05$.

Results

There was no effect of exposure to flavors in milk on the subsequent food preferences of captive coyote pups ($F(2, 6) = 0.50$, $p = 0.6280$). Control pups did not show a preference for either of the flavored foods, and treatment animals did not differ from a no-preference value ($p > 0.2882$) (Table 1). The overall preference value (intercept) for all litters of pups was not different from a no-preference value of 0.50 ($F(1, 6) = 0.45$, $p = 0.5281$).

Coyote pups in this experiment did not have an increased acceptance of food flavored with a rearing flavor when tested against unflavored foods ($F(3, 8) = 2.05$, $p = 0.1861$). Control animals did not have a preference for any of the flavors of kibble offered ($p > 0.2796$) (Table 2). The intercept for all litters of pups was not different from a no-preference value ($F(1, 8) = 0.60$, $p = 0.4626$). Although there was no effect of treatment ($p = 0.1861$) on the behavior of all litters of pups, those raised on anise-flavored milk had a mean preference ratio differing from a no-preference value ($t = 2.48$, $p = 0.0382$) (Table 2). Given that the unflavored ration used in this experiment was identical to the maintenance diet of the animals, this result suggests that pups raised on anise-flavored milk learn to prefer their maintenance ration over that containing the rearing flavor.

An effect due to the sequence of the trial when testing for preferences between the rearing and unflavored diets was also detected ($F(2, 16) = 3.65$, $p = 0.0493$). This effect was due to the development of a stronger preference for the unflavored diet over the course of the 3 trials. The average preference value for the anise-reared litters in Trial 1 was 0.5328, whereas in Trial 3 the average preference value for the same pups had decreased to 0.4008. Only in Trial 3, however, was the mean ratio of the anise litters different from a no-preference value ($t = 4.00$, $p = 0.0001$). It is possible that this preference was learned from experiences obtained with the maintenance ration each day. The biological significance of this result is difficult to ascertain.

Table 1. Mean preference ratios of coyotes reared on anise-flavored, cilantro-flavored, and unflavored milk, when offered anise- and cilantro-flavored kibble in Experiment 1.

Treatment	Mean + SE[a]	95% CI	t Value	p > | t |
Anise-reared	0.5370 + 0.032	0.4592, 0.6148	1.17	0.2882
Cilantro-reared	0.4816 + 0.046	0.3691, 0.5940	-0.40	0.7024
Control	0.5254 + 0.035	0.4406, 0.6102	0.73	0.4912

[a] Treatment means are not statistically different from a no preference value of 0.50.

Table 2. Mean preference ratios of coyotes reared on anise-flavored, cilantro-flavored, and unflavored (control) milk when offered a choice between unflavored kibble and kibble flavored with their respective rearing flavor.

Treatment	Mean + SE	95% CI	t Value	p > | t |
Anise-reared	0.5369 + 0.149	0.5026, 0.5712	2.48	0.0382
Cilantro-reared	0.4727 + 0.024	0.4181, 0.5273	-1.15	0.2815
Control A[a]	0.4989 + 0.020	0.4527, 0.5451	-0.05	0.9576
Control C[b]	0.5218 + 0.188	0.4784, 0.5652	1.16	0.2796

[a] Coyotes offered anise-flavored and unflavored kibble
[b] Coyotes offered cilantro-flavored and unflavored kibble

EXPERIMENT 2

Our second objective was to determine the effect of experience with flavors in solid food on the subsequent food selection behavior of young coyote pups. Research on other animals has shown that initial exposure to solid foods had lasting influences on dietary preference. Goats exposed to blackbrush twigs early in life (between 6 and 26 weeks of age) ate significantly more blackbrush than goats exposed only to alfalfa pellets (Distel and Provenza 1991). Similarly, lambs exposed to flavors early in life established lasting preferences for those flavors (Nolte et al. 1990, Nolte and Provenza 1991).

Methods

Subjects

Test subjects were 22 coyote pups from 6 litters that were hand-reared on unflavored milk replacer. All animals were obtained from the breeding colony at the USDA APHIS WS NWRC Logan, Utah Field Station. The pups were housed in kennels during testing and all trials were conducted during the late morning. Basal rations were made available each day.

Hand-Rearing Procedure

The method of hand-rearing coyote pups was identical to that in Experiment 1 except that all pups were raised on unflavored milk replacer. Pups were randomly assigned to treatment group (i.e., red-berry- or green-apple-flavored kibble) at 5 weeks of age when solid food was first offered. Exposure to the treatments began at the first feeding of solid food. Flavors were added during the milling process of the kibble so the concentration of the flavor within the kibble (i.e., 2.5 kg of flavor concentrate per 1000 kg of feed milled) remained constant throughout the weaning process. Flavors were chosen because they were distinct and could withstand the high temperatures attained during milling. Care was taken that pups were exposed only to the proper treatment food.

Testing Procedure

Preference tests were conducted when pups were 3 and 6 months old. Pups were offered the choice between the rearing diet and novel-flavored kibble. To keep the amount of food consumed per trial relatively consistent between experiments and trials, 100 g of both foods were offered and the pups were given 2 minutes to consume the food. Preferences testing was conducted using a two-choice test as described in Experiment 1.

Statistical Design

Twenty-two pups were randomly assigned to two treatment groups providing 11 pups per treatment. A power analysis using the variance associated with the data from Experiment 1 determined that this sample size was adequate to detect an effect due to treatment. The minimum sample size per treatment was calculated at 7 individuals. The individual preference scores calculated for each pup were used in the statistical analysis. A mixed model, repeated measures ANOVA was used to analyze the data from Experiment 2. The ANOVA had two treatment groups (i.e., pups reared on apple or berry flavored solid food) and individual pups were treated as experimental units. As before, the intercept, least squares means, and confidence interval options were used in the analyses. RATIODIF was also used in the analyses in place of the calculated preference ratios. In all tests, mean preferences were considered different when $p \leq 0.05$.

Results

In both trials, and with both treatments, previous experience with the rearing diet had no effect on subsequent diet selection behavior ($F(1, 20) = 0.15$, $p = 0.7050$). There was no effect of trial sequence on preference ratios ($F(1, 17) = 0.01$ $p = 0.9604$). The intercept for pups in this experiment was not different from a no-preference value ($F(1, 20) = 0.27$, $p = 0.6070$). Means were not different from a no-preference value (Table 3).

Table 3. Mean preference values of coyotes weaned on red-berry- or green-apple-flavored kibble when offered a choice between kibble flavored with their weaning diet flavor and a novel flavor.

Treatment	Mean + SD	95% CI	t Value	p > | t |
Red-berry reared	0.5004 + 0.037	0.4230, 0.5778	0.10	0.9240
Green-apple reared	0.5023 + 0.036	0.4270, 0.5776	0.65	0.5229

GENERAL DISCUSSION

The data collected in these experiments suggested that coyotes did not select solid foods based on experience with flavors they obtained while young, and this result appears to contradict the domestic dog literature. Domestic dogs that experienced a single diet *in utero* through weaning often chose the novel food when presented with a choice in a two-choice test (Ferrell 1984). In this study, however, coyote pups did not select a particular food when given the choice between a familiar and novel food; both foods offered were readily accepted.

It is likely that coyotes do not select foods based on flavor alone. The same conclusion has been made with domestic sheep. Provenza et al. (1995) examined whether increasing familiarity with a flavor increased the consumption of a novel food containing that flavor by sheep. The authors determined that repeated exposure to onion flavor did not affect the intake of novel foods flavored with onion (Provenza et al. 1995).

It is likely that animals select foods based on pairing of flavor with post-ingestive consequences. Most taste aversion studies pair a particular food with an aversive substance causing the animal to associate characteristics of the food with a negative consequence (Burns 1983, Gill et al. 2000, Rudy et al. 1977). In this study, the two foods offered were nutritionally equal, differing only in taste and odor. Neither food was paired with an aversive substance, so both foods offered were presumably associated with only nutritionally and physically positive digestive feedbacks. This may have resulted in the failure of animals to establish preference for diets containing the rearing flavor. Perhaps by pairing the rearing diet with a positive reinforcer (e.g., glucose) and/or the alternative choice with a negative reinforcer (e.g., lithium chloride), pups would begin to show distinct preferences for the rearing diet.

This study provides evidence that flavor cues, independent of other stimuli, are not the sole mechanism driving food selection in coyotes. However, pairing flavor cues with place cues or social influence may be important determinants of diet selection in coyotes. It is possible that coyotes exposed to flavors while in contact with adult conspecifics behave differently than those that were hand-reared by humans. In rats, the presence of adult conspecifics at a feeding site was a strong enough cue to influence the diet choice of the rat pups regardless of the diet cues received during lactation (Galef and Clark 1972). Without the presence of adults, weanling rat pups chose a diet similar to that which was eaten by their mother (Galef and Clark 1972). Scott et al. (1995) found that the relative importance to sheep of the location of preferred foods and social interactions with conspecifics varies, given previous experience with the food items and the individuals in the foraging group. Food preference had more influence on the choice of feeding location when an animal fed with strangers than when it fed with companions (Scott et al. 1995).

Social learning theory suggests that the most effective social models are mothers and respected peers (Bandura 1977). Coyotes raised by their mother in the presence of conspecifics may have different diet selection behavior than those raised without respected peers. Lambs exposed to novel foods in the presence of their mother ate more of the foods after weaning than did lambs that ate with a dry ewe (Thorhallsdottir et al. 1990). Kittens that were fed a protein-deficient diet with the mother cat preferred the deficient diet after weaning even though consuming the diet caused them to be protein deficient (Wyrwicka 1981).

Given the above discussion, future research should focus on the manipulation of flavor cues to alter diet selection (i.e., adding aversive compounds to decrease the consumption of certain food items). Another possible direction for future research would be to elucidate the effectiveness of combining flavor cues with social and visual cues on managing coyote foraging behavior. Because coyotes are social animals, pups learn to hunt with adult conspecifics. Behavior of these adults toward certain prey items may influence the subsequent foraging decisions of their young. Young animals may avoid dietary items that are novel or not consumed by adults. Therefore, altering the flavor cues of a dietary item along with social and visual cues associated with it may impact coyote foraging behavior.

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