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Research Report

THE GENETICS OF DIETARY EXPERIENCE IN A RESTRICTED NATURAL POPULATION

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Abstract—The sources of individual differences in human and non-human animals remain controversial. We demonstrate that diet and genetics interact in determining the ontogenetic trajectory of chemosensory and prey preferences in the common garter snake, *Thamnophis sirtalis*, a dietary generalist. In litters of neonate snakes from a single small field in an earthworm-ingesting population, initial responses to chemical cues from fish and worm were similar, with zero heritabilities. After 12 meals on fish, however, the heritability of both fish and worm chemosensory responses increased markedly, the change in response to fish but not worm chemicals was heritable, the relative preference for fish versus worm was heritable, and the change in relative preference was heritable. In addition, growth rates on each diet were related to changes in chemoreceptive responses. Such genetic-environment variation that emerges only after equivalent ontogenetic experience may be a factor in responses to environmental change in many species.

The evolution of plasticity in behavior is a major concern in recent theory in evolutionary biology (e.g., Schlichting & Pigliucci, 1995; Via et al., 1995; G.P. Wagner & Altenberg, 1996), but psychological interest in the issue goes back at least as far as the Baldwin Effect (Belew & Mitchell, 1996). Measuring genetic-environment interaction in behavioral measures in natural populations has proven difficult (Plomin & Hershberger, 1991), although knowledge of such interactions is critical to understanding how populations adapt to changing circumstances both phenotypically and genotypically. Dietary selection is a major arena for the operation of plasticity, and it is known that variation in both genetics and dietary experience plays an important role in responses to food and food-related cues (Falciglia & Norton, 1994; Segal & Topolski, 1995).

Neonatal garter snakes of the North American natricine genus *Thamnophis* are popular subjects for the study of congenital responses to food cues. Natural diets include earthworms, fish, frogs, salamanders, leeches, slugs, rodents, and birds (Ernst & Barbour, 1989; Rossman, Ford, & Seigel, 1996). Newborn, ingestively naive members of several species in this genus respond to aqueous surface extracts of prey with increased tongue flicking and open-mouth strikes. Species differences in chemosensory preferences in neonates reflect species-typical diets (Burghardt, 1969, 1993). Intraspecific variation reflects microevolutionary processes related to geographic variation in available prey, predators, or interspecific competition for resources (Arnold, 1981; Burghardt, 1970; Burghardt & Schwartz, 1999). The quantitative genetics of these and other behavioral characteristics are well established (Brodie & Garland, 1993). To date, however, all quantitative genetic estimates, including those concerning the number

of generations for population differentiation to occur (Arnold, 1981), are based on the initial responses of snakes at birth. Such calculations may underestimate both the rate of microevolution (Resnick, Shaw, Rodd, & Shaw, 1997) and the role of experience and ontogenetic processes in evolutionary events. For example, in human behavior, the heritability of behavioral and morphological measures increases over years (Hopper & Mathews, 1982; McClearn et al., 1997; Petrill et al., 1998; Plomin, Fulker, Corley, & DeFries, 1997). Controlling the experiences of human subjects over long time spans is most difficult, however, and rigorous experiments are not possible. Typical laboratory rodents are long removed from the natural ecology in which food preferences evolved. Also, in mammals, including people, prenatal and perinatal maternal influences may play important roles in food preferences. Working with garter snakes eliminates such difficulties.

A series of experiments has documented that dietary experience alters the chemosensory prey preferences of young garter snakes (review in Burghardt, 1993), as well as the ability to capture and handle prey (Burghardt & Krause, 1999). Generally, the direction of change is toward increased responsivity to the diet fed or avoidance if the diet is toxic. However, the amount of change, especially in relative preference, seems to vary with individual, species, prey type, and age. Thus, it is possible that variation in the response to prey experience is itself genetically controlled. To assess the stability of genetic effects on chemosensory prey preference, we tested neonatal snakes from a single population at birth and after 6 weeks of dietary experience on the same diet.

METHOD

Pregnant female eastern garter snakes, *Thamnophis sirtalis*, captured over a few days during June in a field on Beaver Island, Charlevoix County, Michigan, were moved to the laboratory. Beaver Island, the largest island in Lake Michigan, contains great numbers of garter snakes. Diet studies of wild snakes on Beaver Island show that more than 85% of the diet consists of earthworms, and fish have never been recorded as part of the diet (Gillingham, Rowe, & Weins, 1990).¹ Yet snakes on smaller nearby islands in the archipelago apparently do eat both fish and tern nestlings that smell like fish (Greenwell, Hall, & Sexton, 1984). In fact, mainland populations of this species are known to frequently invade fish hatcheries and otherwise exploit novel prey (Gregory & Nelson, 1991).

The females from Beaver Island were maintained in the laboratory on a diet of mixed fish and worms until they gave birth. On the day of birth, the neonates were separated, sexed, weighed, measured, and

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1. The pregnant female snakes were captured in a 1-ha field immediately west of East Side Drive near a small creek called the Jordan River. This population eats earthworms almost exclusively, along with the occasional toad (J.C. Gillingham, personal communication, June 1991).

housed individually in identical plastic gel boxes (18 × 13 × 5 cm) containing a cage liner substrate, a petri dish with water, and a shelter made from a folded piece of substrate liner. The temperature was maintained at 23 to 25 °C. Beginning at 7 days of age, all animals were tested on their responses to mosquito fish (*Gambusia affinis*) and earthworm (*Lumbricus terrestris*) aqueous-prey chemical substances presented on cotton swabs using standardized methods developed over the years in several laboratories (review in Burghardt, 1993). The standardized aqueous-based stimuli were tested full strength and at 10⁻² and 10⁻⁴ dilutions along with a deionized water control. The tests were performed in the following sequence: On Day 7 after birth, all snakes were tested with water and the increasing concentrations of the fish extract, with the full strength extract tested twice. Each trial took a maximum of 30 s, and at least 20 min elapsed between trials. The following day, the testing was repeated with the earthworm series. A week later, the fish and earthworm tests were repeated again on successive days. Additional animals were tested to evaluate changes in responsiveness due to repeated testing alone.²

The day following the completion of all four rounds of testing, all snakes were given their first meal of live mosquito fish in a videotaped trial. After this feeding, the snakes were given 11 more bi-weekly feedings on live fish. The snakes were then weighed and measured, and the chemoreceptive tests were repeated in the same format as before, beginning 7 days following their last meal. Following these tests, the snakes were again given a videotaped fish-feeding trial, followed by four preference tests in which they were offered a choice between several live fish and equivalent-sized pieces of earthworm.

The experimental animals were derived from 17 litters, and 79 individuals (38 males and 41 females) completed both rounds of testing. The chemoreceptive responses were scored using a procedure combining tongue flicks directed at the stimuli and attack latency in a Tongue Flick–Attack Score for repeated measures, or TFAS(R) (Cooper & Burghardt, 1990).³ All scores were natural log transformed after adding 1.0 to each score to eliminate heteroscedasticity. There were two scores for water and four scores for full-strength fish extract and two scores for water and four scores for full-strength worm extract before feeding experience and the same number after feeding experience. Each set of four full-strength-prey-extract scores was highly repeatable (Lessells & Boag, 1987), and these sets were used in the analyses reported here.⁴ Scores were averaged for each stimulus type

2. An additional 12 animals randomly drawn from four litters were used as controls. All chemoreceptive tests in this group were performed using water only, so that the effects of using ascending concentrations of prey chemicals could be assessed. Before feeding, these snakes responded to the aqueous stimuli at low levels and showed no change over trials in a session; if anything, there was a decrease. After feeding experience, these snakes showed a general overall increase in response, but again there were no changes across trials to indicate increasing responsiveness as trials progressed. Thus, any increased responding across trials in a session by the experimental subjects can be attributed to the increasing concentrations of chemosensory stimuli and not to order effects within sessions.

3. If no attack occurs in 30 s, TFAS(R) equals the number of tongue flicks directed at stimulus. If an attack occurs, TFAS(R) is calculated as follows: maximum number of tongue flicks directed at stimulus in any trial + (30 – attack latency). The rationale and psychometrics are reviewed in Cooper and Burghardt (1990).

4. Repeatabilities for the four tests in each of the four conditions (fish and worm before and after fish feeding) ranged from 0.59 to 0.68.

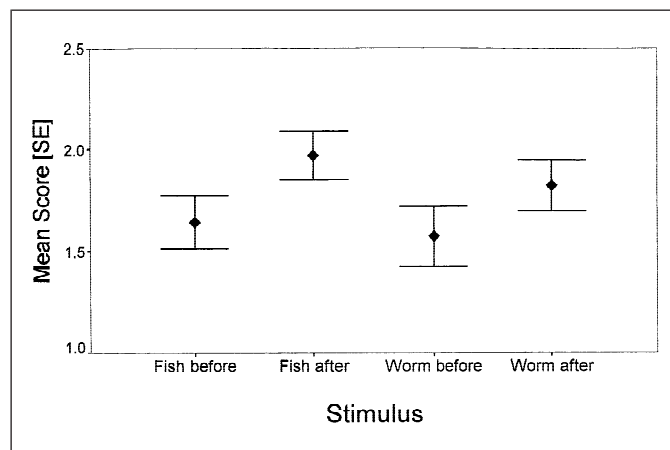


Fig. 1. Tongue Flick–Attack Scores of 79 neonatal *Thamnophis sirtalis* to aqueous fish and earthworm chemical prey stimuli presented before and after 12 meals on fish.

before and after dietary experience. Relative preference scores were derived by subtracting worm scores from fish scores both before and after feeding experience. Changes in fish and worm scores were derived by subtracting early (prefeeding) from late (postfeeding) results for each prey stimulus. Changes in relative preference were calculated by subtracting the early relative-preference scores from the late relative-preference scores. Heritabilities were calculated using maximum likelihood methods with sibship scores.⁵ Although we have found multiple paternity in some populations of this species (Schwartz, McCracken, & Burghardt, 1989), this would only increase somewhat the heritabilities reported. We determined the significance of heritabilities using likelihood ratio tests referenced to a chi-square distribution with one degree of freedom. The obtained probability value was divided by two because of the restriction that maximum likelihood estimates of heritabilities cannot be negative.

RESULTS

Both initially and after fish diet experience, the snakes responded much more to prey extracts than to water. Initially, fish and worm extracts were responded to almost equally (see Fig. 1), but only the response to fish increased significantly after feeding experience, $t(78) = 2.79, p < .01$, for fish extract and $t(78) = 1.65, p > .10$, for worm extract. In contrast to previous reports on other species or populations (Brodie & Garland, 1993), the data demonstrated no significant heritability of initial responses to either fish or earthworm extracts (Table 1). This result could be due to the small source population of the females and their concentration on a single prey type (earthworms) for many generations. However, after experience with a fish diet, snakes retested in exactly the same manner evinced a significant heritability

5. See chapters 26 and 27 from Lynch and Walsh (1998), as well as Shaw (1987) and Hopper and Mathews (1982). We treated sibships as if all members had the same paternity, so the expected additive genetic correlation between any members of the sibship was .5. As we were measuring narrow sense heritabilities, we ignored the dominance covariance between sibs. Dominance effects are consequently treated as part of the total phenotypic variance. We also considered each sibship as being unrelated to all other sibships, so that the expected additive genetic correlation across different sibships was zero.

Table 1. Heritability of chemoreception measures based on full-strength fish and worm stimuli before and after 12 feedings on fish

Chemosensory measure	h^2	Standard error	p value
Fish before	0.000	0.291	n.s.
Worm before	0.000	0.219	n.s.
Fish after	0.323	0.231	$p < .05$
Worm after	0.497	0.245	$p < .005$
Change in fish response	0.226	0.178	$p < .05$
Change in worm response	0.160	0.157	n.s.
Preference (fish – worm) before	0.074	0.151	n.s.
Preference (fish – worm) after	0.532	0.230	$p < .0005$
Change in preference	0.263	0.211	$p = .05$

Table 2. Correlations (Spearman, r_s) of growth-rate measures with prey chemoreceptive scores before and after 12 feedings on fish

Chemosensory measure	Snout-vent length	Mass
Fish before	.297**	.237*
Worm before	.331**	.349**
Fish after	.264*	.314**
Worm after	.083	.133
Change in fish response	–.050	.012
Change in worm response	–.235*	–.227*
Preference (fish – worm) before	.035	–.104
Preference (fish – worm) after	.248*	.249*
Change in preference	.198	.258*

* $p < .05$. ** $p < .01$.

of response to both fish and worm. That this was not simply an increase in responsivity is shown by the fact that the change in fish response was heritable, but the change in worm response was not. Furthermore, the relative preference (fish score – worm score) was not heritable before fish experience but was heritable after experience. In addition, the change in the relative prey preference was itself heritable. Although raw scores did show a significant sex difference in overall response rate, with females more responsive than males, this did not carry over to the difference scores. Calculating heritability with aqueous-control scores subtracted from full-strength-extract scores and with sex taken into account did not alter the pattern of results.

These results clearly show that the experience with fish was processed differently by the individual snakes and that the experiential effect was heritable. Thus, the ability to utilize experience in altering perceptual responses to prey is under genetic influence in a population existing on a narrow diet. This appears to be the first such demonstration in a natural population.

As expected, high heritabilities were calculated for mass and snout-vent lengths, undoubtedly affected by maternal factors. In chemosensory prey preference, however, maternal and maternal-diet effects do not seem to play a role (Burghardt, 1993). Over the course of the experiment, the snakes increased in mean mass from 2.15 to 3.74 g and in mean snout-vent length from 167 to 195 mm. Although the heritability of mass and length did decline after dietary experience, both heritabilities were still substantial and significant (mass: 0.72 ± 0.25 ; length: 0.44 ± 0.24). Across all snakes, there were significant correlations between both growth measures and initial worm and fish chemosensory preference (Table 2). After dietary experience, only the correlation with fish preference remained significant. The change in worm, but not fish, chemosensory preference was negatively related to growth rate. Relative fish preference after feeding on fish was significantly related to growth, but the same measure before feeding had no predictive power. The change in relative fish preference correlated significantly with growth in mass. The amount of fish eaten by all animals was virtually identical. These data suggest that the sensory bias for the change in prey preference is related to the ability of the animals to utilize the diet effectively, which itself differs among individuals in a population.

DISCUSSION

The prey-choice tests following the final chemosensory tests revealed that virtually all snakes, which only had fish to eat, preferred fish to earthworms at the end of the experiment. The chemosensory responses showed, however, that the phenotypic expression of behavior might mask an underlying sensory preference. Because snakes with higher chemoreceptive responses to worms grew less well than those snakes that developed a chemosensory bias for fish, a strong, unexpected link between perception, experience, diet quality, and growth is supported (Lyman-Henley & Burghardt, 1995). This research has an application to conservation efforts because it demonstrates that the underlying genetic structure of a population may be critical to selecting animals most suitable for reintroduction in habitats with ecologies somewhat different from the source population.

That snakes from an earthworm-eating population so readily shift to fish raises the issue of the evolutionary origin of this ability. The ancestral species that gave rise to the North American natricine snakes (*Thamnophiini*) may have been amphibian and fish specialists similar to the water snakes (*Nerodia*; Rossman et al., 1996). Prior work on dietary-generalist garter snakes has shown that they grow better on fish than on earthworm diets (Scudder-Davis & Burghardt, 1987). This may be due to the relative lack of calcium in the worms, as calcium is needed for adequate bone growth in many snakes. When mineral substances are added to earthworms, growth-rate differences due to diet are greatly reduced (Lyman-Henley & Burghardt, 1995). Thus, during the crucial period of maximal growth, snakes may quickly learn to take the diet that provides better nutrition. A genetic basis for substantial phenotypic plasticity may be one means by which a generalist species adapts to varying habitat situations. The common garter snake is the most wide-ranging and successful snake species in North America (Rossman et al., 1996), with many insular populations. It may prove to be a valuable model for testing recent theoretical predictions on age and experience-specific patterns of genetic variance (Promislow, Tatar, Khazaeli, & Curtsinger, 1996) underlying the evolution of plasticity (A. Wagner, 1996).

The data presented here demonstrate that when members of a highly precocial species are raised on the same diet, genetic effects on feeding behavior differ across age. This age-related pattern of genetic effects occurred in families of neonates drawn from a restricted popu-

lation with a limited natural diet. Additionally, the manner in which experience is processed can differ because of genetic factors, and these effects link both sensory food preferences and metabolic utilization in growth. Such linkages might be both common and important in many species, but have been difficult to study in traditional laboratory animals and people.

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