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15 Genetics, Plasticity, and the Evolution of Cognitive Processes

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In this volume the emphasis has been on the diverse cognitive abilities of animals; the various ways that they can be studied both in the field and in captivity; and on theoretical issues as to the number, kinds, mechanisms, and comparative distribution of such abilities. It is now generally accepted that cognitive abilities have evolved just as have other characteristics of animals, such as anatomical structures. If natural selection produces animals with abilities to cope with problems in some areas of their lives better than in others, we need to focus on the different abilities animals possess and the contexts in which they are expressed. Moreover, for cognitive abilities to evolve, individuals in a population must differ in their cognitive abilities (or in the processes underlying them) and these differences must have adaptive consequences. Rarely, however, has work on these issues been carried out using modern methods of quantitative genetics in nondomesticated species, and yet such work may be particularly useful.

The evolution of cognitive abilities can be considered a subset of the evolution of plasticity in behavior. Behavioral plasticity has recently become a major concern in evolutionary biology (e.g., Via et al. 1995), but psychological interest in the issue goes back at least as far as the ''organic selection'' promulgated in the late nineteenth century (Belew and Mitchell 1996). In this effect, selection acts on plasticity itself. At the time, this mechanism was viewed as an elegant means of dealing with the then still-potent Larmarckian views of many scientists who could not envision how natural selection for either instincts or structures could explain the diversity found in nature without the inheritance of acquired traits.

Romanes (1883) and other theorists such as Herbert Spencer developed the neo-Lamarckian lapsed intelligence theory. This theory aimed to explain how instinctive or hardwired behavior could have evolved by postulating that initially such behavior was experience dependent or learned, then was subsequently encoded in the hereditary material and transmitted as inherited ''instinct.'' In essence, the noncognitive evolved from the cognitive in terms of behavior, turning the typical evolutionary scenario on its head. Although the major thrust of organic selection was independently discovered by several eminent scientists (i.e., Baldwin, Poulton, and C. Lloyd Morgan) about 1896, today it is often simply called ''the Baldwin effect'' (see Belew and Mitchell 1996). Waddington's theory of genetic assimilation (Waddington 1953) was a much later model in this vein, and other more recent ones have been collected in Belew and Mitchell (1996).

However, attempts to study the Baldwin effect empirically, rather than through simulations and models, has proven difficult. One reason for the difficulty is that measuring a gene–environment interaction through behavioral changes in natural populations is difficult (Plomin and Hershberger 1991), although knowledge of such interactions is critical to how populations adapt to changing circumstances both phenotypically and genotypically. In many species 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 (e.g., Burghardt 1993).

There are many reasons for the lack of research on the genetic bases of individual differences in cognitive abilities. First, comparative psychology was historically focused on species differences in ''intelligence'' and on ranking animals along some continuum. Here the search was for a key method that could produce a reliable indicator of intelligence across species; it assumed that there was such a single indicator if we could only discover and measure it.

Second, genetic studies require large numbers of animals that have been raised and tested identically, and this is hard to accomplish with dogs, monkeys, cats, pigeons, and other typical laboratory animals. Small samples of animals of diverse genetic backgrounds were tested intensively and individual differences dismissed as noise or the effects of pretraining experiences, if they were noted at all. Species that could be reared and tested in large numbers were laboratory mice and rats, and these were typically strains or breeds quite highly inbred, so genetic differences were minimal. Crosses between breeds and selective breeding did show a genetic basis, as demonstrated in the pioneering studies on dogs by Scott and Fuller (1965), but factors such as temperament and sensory function seemed to preclude a measure of ''pure'' intelligence and so such work fell into disfavor.

Recently, however, studies on the role of specific genes in behavior, including learning, exploration, and motivation, by adding and eliminating specific genes in inbred animals, have renewed interest in the genetic basis of individual differences in behavior within a population (Tang et al. 1999). Quantitative trait locus (QTL) methods are also being used to specify where genetic influences on certain traits are located on chromosomes. Such studies appear to hold promise for the genetic study of specific phenotypic attributes, but so far are limited to highly domesticated species or those for which extensive gene sequencing and pedigree data are available.

In my laboratory, we have focused on two biologically important areas where experience may play an important role—obtaining food and avoiding becoming food. We wanted to do this using fairly natural problems that an animal might need to solve in order to survive. We also wanted to use a species in which postnatal parental care and influence are minimal, and thus from birth individuals have to solve problems on their own or perish. It was also important to be able to obtain large numbers of animals from the same population so that natural levels of genetic variation could be studied; ample evidence shows that geographical variation in behavior can be considerable (Foster and Endler 1999).

My work over many years on the behavior of snakes, particularly newborn or newly hatched snakes, led me to decide that snakes would be an ideal group to study for the quantitative genetics of basic cognitive processes. Ectothermic reptiles are not generally considered ideal subjects for the study of animal cognition, although there is a long history of their use in learning and discrimination studies (Burghardt 1977). Snakes, however, have a rather dismal success record in traditional learning paradigms in the old literature, primarily because their perceptual world and effector operating space are so alien to ours (Rivas and Burghardt 2001). In addition, it is because of the highly precocial and seemingly hardwired behavior of young snakes that their ability to learn has been neglected. Yet, neonatal snakes do satisfy the advantages listed above in terms of genetic studies. Furthermore, although their behavior is highly constrained by the absence of limbs and, for most species, a great reliance on chemosensory cues, snakes are surprisingly diverse and successful animals (Greene 1997).

While no one would claim they are as cognitively complex as mammalian carnivores and primates, snakes do possess a series of behavioral adaptations that are only beginning to be studied experimentally. For example, the death feigning of hognose snakes is triggered by the presence of a ''predator,'' and recovery is more rapid if the predator, though present, is not gazing directly at the snake (Burghardt 1991). Many young snakes have tail tips with white or yellow markings that are used to lure unsuspecting prey; for example, hatchling Malayan pit vipers, *Calloselasma rhodistoma*, would raise their tail tips and slowly wiggle them in the presence of insectivorous lizards (G. M. Burghardt, Jones, and Schwartz unpublished observations). They would not do so in the presence of mice, although they

would eat both kinds of prey. The diversity and complexity of such tail luring behavior has been recently reviewed (Reiserer in press). The use of the tail, not only as a lure, but also as a distraction display to cause a potential prey item, such as a rodent, to momentarily turn toward a rustling leaf and away from the snake's head approaching from a different direction, has been documented experimentally (Mullin 1999). There are also many anecdotal accounts of other tactics used by snakes in locating the nests of birds and turtles, homing, and so on (e.g., Mori et al. 1999). More traditional tests of snake learning, such as spatial tasks, are also being reported (e.g., Holtzman et al. 1999).

Particularly amenable to quantitative analysis are behavior patterns used repeatedly, such as the responses made by neonatal snakes to simulated predators, and the behavior involved in identifying, capturing, subduing, and swallowing prey. For many years we have studied the behavior of neonatal, young, and adult snakes, primarily natricine snakes in the family Colubridae. In North America, this family consists of "highly derived and recently evolved snakes" (Holman 2000). Natricines include the common water (*Nerodia*) and garter snakes (*Thamnophis*) of North America and their many East Asian relatives. All the New World natricines are viviparous and often have large litters, which facilitates genetic studies.

Avoiding Predation

Neonatal natricine snakes lack parental care and are typically small and vulnerable to predation. Natural selection should thus foster deployment of whatever cognitive ability a small snake might possess to the task of survival. Natricine snakes exhibit several antipredator behavior patterns, such as flight (including reversing direction), threatening (body or neck flattening, hissing, striking, slow-motion tongue flicking), and biting. When contacted by a predator, they may

writhe, wrap around the interloper, emit and rub a vile musk on the predator, or defecate. They may also hide their head and wave their tail, seemingly to direct the predator to their least vulnerable part. Both adult and neonatal snakes may have species-typical repertoires (Scudder and Burghardt 1983; Herzog and Burghardt 1986; Bowers et al. 1993). Within a population, the behavior of individual neonatal snakes may also differ at birth, and these temperament or personality differences appear to be heritable (Arnold and Bennett 1984; Brodie and Garland 1993) and can be remarkably stable (Herzog and Burghardt 1988).

The defensive behavior of snakes is not fixed at birth, however. There are changes that may occur over the first weeks of life, and these ontogenetic trajectories also vary by species (Herzog et al. 1992). Furthermore, experience does affect these responses. We discovered that littermates that were handled differently because they were used in different studies were more or less defensive than those given minimal handling (Herzog and Burghardt 1988). Young snakes tested with repeated but controlled contact stimulation for a short period on one day were much more defensive 2 weeks later, suggesting considerable retention if the appropriate test is utilized (Herzog 1990).

However, there was also evidence of genetic involvement in the response to repeated stimulation. Both short-term and long-term habituation were documented in garter snakes and we found differences in habituation processes both within and between species (Herzog et al. 1989). When short-term habituation trials were carried out in young snakes at day 1 and day 60, the slopes of the curves were remarkably consistent and, even more remarkable, the shapes of the curves were themselves consistent (Bowers 1992; B. B. Bowers and G. M. Burghardt, unpublished observations). All this evidence suggests that the way snakes process experience is under genetic control, down to the shape of their learning

curves. Such studies, however, do not help elucidate the nature of the gene–environment interactions involved. To begin to study this issue, we turned to aspects of foraging behavior.

Finding Prey

Just as with antipredator behavior, neonatal natricine snakes have species-typical innate responses to the chemical stimuli of prey at birth as well as precocial prey capturing abilities (see the reviews in Burghardt 1993; Burghardt and Schwartz 1999). The latter also show plasticity in early ontogeny (Krause and Burghardt 2001), but only the responses to food chemicals will be discussed here.

The most popular groups for the study of congenital responses to food cues are neonatal garter snakes of the North American natricine genus *Thamnophis*. Natural diets can include earthworms, fish, frogs, salamanders, leeches, slugs, small mammals, and birds. Newborn, ingestively naive members of several species of this genus respond to aqueous surface extracts of prey with increased tongue flicking and open-mouthed strikes. The quantitative genetics of these and other behavioral characteristics are well established (Brodie and Garland 1993). Before our work, however, all quantitative genetic estimates were based on the initial responses of snakes at birth. Such calculations may underestimate both the rate of microevolution (Resnick et al. 1997) and the role of experience and ontogenetic processes in evolutionary events. For example, in humans, the heritability of behavioral and morphological measures increases over years (Petrill et al. 1998).

Snakes have to make many decisions when foraging, and one of the most critical is whether to attack a prey animal when one is encountered. Many studies have shown that postnatal dietary experience can alter the chemosensory-elicited tongue flicking and prey attack responses of young garter snakes (Burghardt 1993). Gener

ally 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 preferences, seems to vary with individuals, species, prey type, and age of the individual. This led me to consider whether variation in how snakes respond to prey experience is itself genetically controlled.

We studied the common garter snake, *Thamnophis sirtalis*, the most wide-ranging and successful snake species in North America. This success may be due to the fact that the species is a prey generalist, feeding on almost every prey type recorded for any of the more than thirty garter snake species. The species is also known for its ability to invade areas with introduced food resources, such as fish hatcheries, where snakes living largely on earthworms shift to the new diet quite quickly and do better on it than on the natural diet (Gregory and Nelson 1991). To assess genetic effects on chemosensory prey preferences and their modification, neonatal snakes from 17 litters in a single population ($n = 79$) were tested at birth and after 6 weeks on the same diet (details in Burghardt et al. 2000).

Pregnant female eastern garter snakes, *Thamnophis sirtalis*, captured over a few days in small field on Beaver Island in upper Lake Michigan, were moved to the laboratory. Beaver Island contains great numbers of garter snakes and their diet is almost exclusively earthworms (*Lumbricus terrestris*), while ingestion of fish has never been recorded. Snakes from all litters were reared from birth exclusively on mosquito fish (*Gambusia affinis*). After birth, the animals were measured and then tested on their responses to mosquito fish and earthworm aqueous prey chemicals, along with control stimuli (water), presented on cotton swabs using standardized methods (see review in Burghardt 1993). Each trial took a maximum of 30 seconds.

Following the completion of four rounds of testing, all snakes were given twelve meals of live mosquito fish twice a week. All the snakes were

again measured and the chemoreceptive tests repeated in the same format as before. The chemoreceptive responses were scored using a standard procedure. The scores for water and fish and worm replicates before the feeding experience were combined, as were those for the responses after dietary experience. Relative preference scores were derived by subtracting worm scores from fish scores both before and after the feeding experience. Fish and worm change scores were derived by subtracting early (prefeeding) from late (postfeeding) results for each prey stimulus. The change in relative preference was calculated by subtracting the early relative preference scores from the late relative preference scores. Heritabilities were calculated using maximum likelihood methods with sibship scores, and only significant values are reported below.

Both initially and after the fish diet experience, the snakes responded much more to prey extracts than to water. Initially fish and worm extracts were responded to almost equally, but after the feeding experience, only the response to fish increased significantly. In contrast to previous reports on other species or populations (Brodie and Garland 1993), there was no significant heritability of initial responses to either fish or earthworm extracts. However, after the fish diet experience, snakes retested in exactly the same manner now evinced a significant heritability of response to both fish (0.32) and worms (0.50). That this was not simply a general increase in responsivity to all extracts is shown by the fact that the change in the fish response was heritable (0.23), but not that to worms (0.16). Furthermore, the relative preference (fish score − worm score) was not heritable before the fish experience (0.07), but was heritable after this experience (0.53). In addition, the change in the relative prey preference was itself heritable (0.26).

These results clearly show that 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 natural population existing on a narrow diet. This appears to be the first such demonstration in a natural population.

This heritable plasticity in chemosensory prey preference had other effects that support the adaptive nature of such plasticity. Over the course of the experiment, the snakes grew significantly in mass and length. It is interesting that across all snakes there were significant positive correlations between growth measures and initial worm and fish chemosensory preferences (the results are reported below only for mass; body length results were very similar). After their dietary experience, however, only the correlation with a fish preference remained significant (fish: $r_s = 0.31$; worm: $r_s = 0.13$). On the other hand, the change in worm ($r_s = -0.23$), but not fish ($r_s = 0.12$) chemosensory preference was negatively related to the growth rate. Relative fish preference (fish − worm scores) after the snakes fed on fish was significantly related to growth ($r_s = 0.25$), but the same measure before feeding had no significant predictive power ($r_s = -0.10$). The change in this relative fish preference from before to after dietary experience was significant for growth in mass ($r_s = 0.26$).

Since all the snakes ate virtually the same number of fish, these data suggest that the sensory bias for the experiential effect on prey preference is positively related to the ability of the animals to utilize the diet effectively, which itself differs among individuals in a population. Since 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 and Burghardt 1995).

Future Directions

The study of genetic contributions to cognition is no simple matter. For example, multiple pater-

nity occurs in this species (McCracken et al. 1999), and this would increase somewhat the heritabilities reported here. A litter can thus be composed of full and half siblings. Use of this trait and molecular genetic methods for identifying full and half siblings within a litter allows comparisons of two full sibships produced by the same mother at the same time and with the same maternal traits, such as body size, nutrition, stress, and body temperature. The application of this method to some morphological and behavioral traits in neonatal common garter snakes resulted in a better resolution of the genetic contribution through a comparison of paternal and maternal genetic contributions plus environmental effects (King et al. 2001). This method has yet to be applied to the chemosensory preference changes described earlier.

If the ability to profit by experience is an adaptive trait, with both costs and benefits depending on the context, then determining individual differences in such plasticity requires quantitative study in naturalistic contexts. Animals face many recurring problems and among the most important of these are avoiding predators and implementing the series of decisions needed to locate, capture, and ingest prey or other food reources. All animals face similar problems.

Genetic differences clearly underlie the plasticity of snake behavior in response to variable and ecologically relevant experiences. Furthermore, the heritable plasticity to shift behavior to favor novel prey types is related to the ability of snakes to metabolically utilize the relevant resource, in this case fish. This finding demonstrates that the traits underlying behavioral plasticity and cognitive processing are profoundly integrated into the entire biology of the species. If this is true in snakes, the importance of studying genetic and individual differences along with cognitive ethology may be even greater, although much more difficult, with nondomesticated mammals and especially primates.

Scattered throughout much of the primate literature is ample evidence that great individual differences in behavior, temperament, social prowess, and cognition exist. Often great claims are made on the basis of the accomplishments of a particular "star" subject: chimpanzee, dog, monkey, or parrot (Bekoff 1998). However, until the underlying basis and consequences of such differences, *and their variation*, are understood, it is unlikely that a detailed analysis of the evolution of cognitive abilities will be possible.

Acknowledgments

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