

**Developmental Behavior
Genetics: Neural, Biometrical,
and Evolutionary Approaches**

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Inheritance and the Evolution of Behavioral Ontogenies

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Developmental behavior genetics is the intersection of developmental and genetic studies of behavior. The principle focus in this new field is on how gene action changes during development and on how heritabilities and genetic correlations change with age (De Fries & Fulker, 1986; Plomin, 1983, 1986).

The evolutionary genetics of behavioral ontogenies is a still newer and relatively unexplored subject. Here the focus is on the inheritance and evolution of the program for behavioral development. My thesis is that this new field will grow faster if it fosters contacts with surrounding disciplines. In this chapter I review some relevant concepts of quantitative genetics and evolutionary theory and then examine three phenomenological examples of possible contacts: alternative male mating tactics, ecological niches, and birdsong. My aim, then, is to consider how our understanding of the evolution of these phenomena might be enhanced by focusing on the inheritance of behavioral ontogenies. These examples also have a transcendent interest to the student of developmental genetics for they suggest how an evolutionary perspective can be used to focus genetic work.

BACKGROUND

To conceptualize the genetic issues, it will be helpful to use an idealized behavior with a simple ontogeny. Such a case is shown in Figure 9-1. In this hypothetical example the average value of the behavioral trait increases linearly with age, but any regular pattern of change could be used to illustrate the following points. Suppose we score the behavior in a large sample of individuals at each of three ages. We could then define three age-specific traits (e.g., behavior at age 1). Plotting our hypothetical data, we find that each of these age-specific traits shows a continuous distribution, as illustrated in Figure 9-1.

Two Concepts from Quantitative Genetics

Some important conceptual tools from quantitative genetics will enable us to visualize the inheritance of behaviors that change during ontogeny. The first important

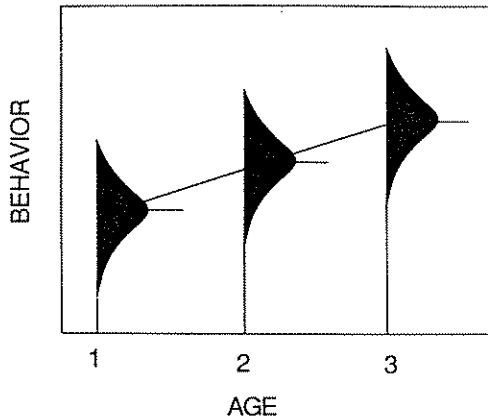


Figure 9-1 A hypothetical behavior whose average value (horizontal lines) increases with age. The bell-shaped figures are frequency distributions portraying the behavioral variation among individuals at each age.

tool is *genetic variance*, which describes the degree of hereditary resemblance between parents and offspring in some phenotypic trait. In Figure 9-2 we see the average scores of offspring at age 1 plotted against the average scores of their parents at that same age. The data points in the example show a linear trend that might reflect Mendelian inheritance as well as the effects of environmental features that are shared by families. Let us imagine that such common environmental effects have been eliminated or disrupted by experimental design (e.g., by cross-fostering of offspring) so that the observed resemblance between offspring and parents can be wholly attributed to inheritance. In this case, we can show with a little algebra (Falconer,

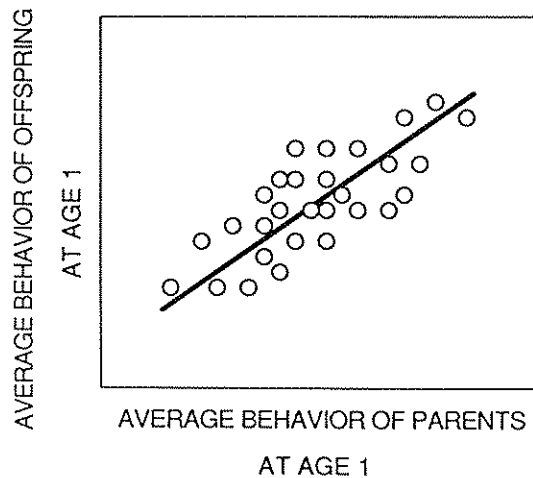


Figure 9-2 Hypothetical data showing the average behavior of offspring at age 1 plotted against the average behavior of their two parents at that same age. The slope of the least squares best-fit line estimates the heritability of behavior at age 1.

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1981, Chapter 9; Fisher, 1918) that the resemblance is due to a particular additive property of gene action. The property that measures offspring-parent resemblance in a particular trait is known as *additive genetic variance*. *Heritability* is simply a standardized genetic variance that varies between zero and one. The slope of the least-squares line in Figure 9-2 estimates the heritability of behavior at age 1.

Extending our approach to the behavior as it is expressed at other ages, we could likewise estimate the heritability of behavior at any age. We could then summarize our findings by graphing genetic variance or heritability as a function of age. Such profiles of genetic variance are the first critical type of genetic information needed to predict response to deliberate or natural selection. But before we consider the role of genetic variance in evolutionary prediction, let us examine the second critical type of genetic information.

The second important genetic issue is hereditary correspondence between behaviors expressed at different ages. Two extreme possibilities are shown in Figure 9-3, in which the average behavior of offspring at age 2 is plotted against the average behavior of their parents at age 1. As before, nongenetic causes of resemblance

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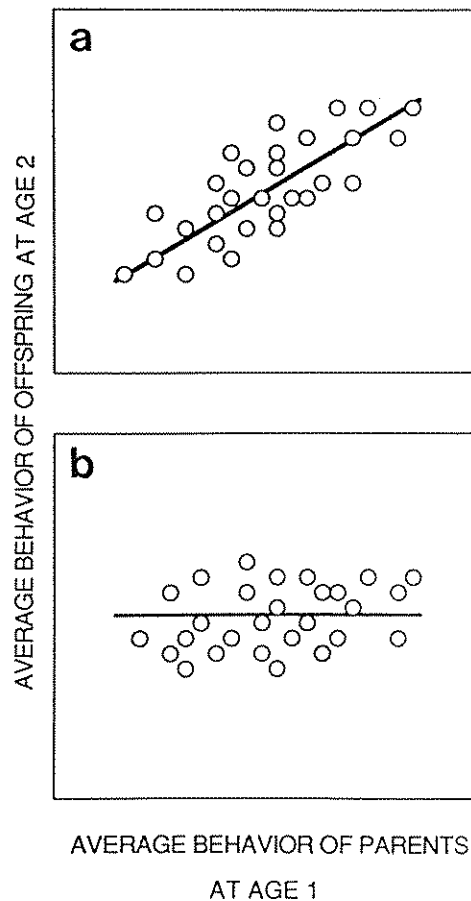


Figure 9-3 Hypothetical data illustrating two extremes of genetic covariance of behavior as it is expressed at two different ages. (a) Strong positive genetic covariance between behavior at age 1 and the same behavior at age 2. (b) Lack of genetic covariance.

between offspring and parents have been disrupted by experimental design. One possibility is that the resemblance between relatives in behaviors expressed at different ages is as strong as the resemblance in behaviors expressed at the same age (compare Figure 9-3a with Figure 9-2). This circumstance could arise if virtually the same genes were responsible for genetic variation in behavior at the two ages. Alternatively, a wholly different set of genes might affect behavioral differences at age 2. In this case there might be no average resemblance between parent and offspring behavior at the two ages (Figure 9-3b). Eaves and colleagues (Chapter 13) refer to this distinction as a contrast between situations in which genes act all the time versus situations in which genes are occasion or age specific.

The genetic parameter that describes hereditary correspondence between behaviors expressed at different ages is called *genetic covariance*. These covariances are often standardized so that they vary between minus one and plus one; they are then known as *genetic correlations*. The situation in Figure 9-3a with strong hereditary resemblance reflects a large, positive genetic covariance between genetic values for behavior at ages 1 and 2. The lack of resemblance in Figure 9-3b reflects a zero genetic covariance between genetic values for behavior at the two ages. Genetic coupling, described by genetic covariance, can arise from pleiotropy or linkage disequilibrium (Falconer, 1981; Hazel, 1943).

Genetic variances and covariances are convenient descriptors of hereditary resemblance in behavior. Because these genetic parameters describe behavioral transmission from one generation to the next, they are also the critical hereditary variables needed to make evolutionary predictions. The elementary evolutionary issue, after all, is to make a prediction about how behavior will change from one generation to the next. To make such a prediction we need, aside from inheritance, a specification of selection. Selection describes how the parentage of the next generation is biased; inheritance (genetic variances and covariances) describes how that bias is transmitted.

Evolutionary Response to Selection on Behavior

Selection acting at a particular age can cause evolution not only of behaviors expressed at that age but also of behaviors that are expressed at other ages (Falconer, 1981, Chapter 19). Let us consider the simple case of so-called truncation selection. Imagine that selection acts on behavior at age 1 so that only a subset of potential future parents actually survives to produce offspring. For example, suppose that only parents above some critical behavioral score actually produce offspring. If behavior at age 1 is heritable, those parents will leave offspring whose behavior at age 1 has higher scores than the behavior of average offspring of all potential parents (Figure 9-4a). That behavioral discrepancy between the offspring of selected parents and of all potential parents is known as the *direct response to selection* on behavior at age 1. Likewise, if the genetic covariance between behavior at age 1 and 2 is nonzero, selection on behavior at age 1 will produce a *correlated response* in behavior at age 2 (Figure 9-4b). By computing the direct and correlated responses to selection for each generation we can deduce the long-term evolutionary trajectory of the population and inquire about the long-term effects of genetic correlation.



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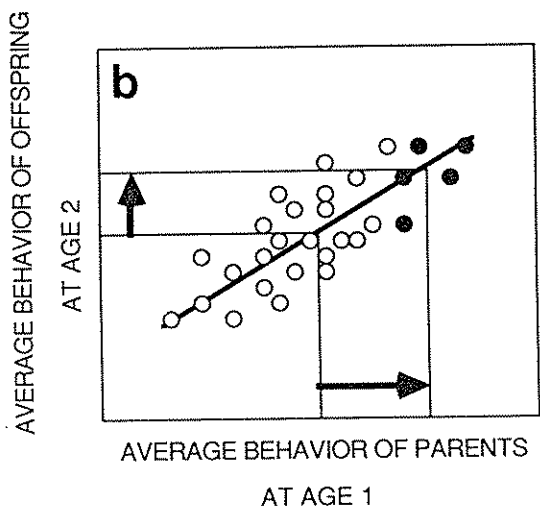
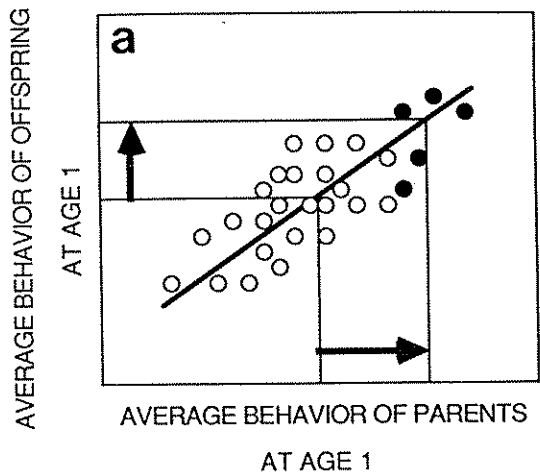


Figure 9-4 The evolutionary response to selection on behavior. (a) Same hypothetical data as in Figure 9-2, with heritability equal to the slope of the heavy line. The average behavior of all potential parents is indicated by the vertical line at the center of the figure. The expected behavior of the average of all potential parents is indicated by the horizontal line at the center of the figure. If selection acts on the parental generation we can readily predict the evolutionary response. If only the five sets of parents with the highest average behavioral scores become the actual parents of the next generation, the expected behavior of their offspring is indicated by the uppermost horizontal line. The horizontal arrow indicates the strength of selection (the difference between potential and actual parents). The vertical arrow indicates the response to selection (the consequence of the imposed selection, assessed in the next generation). (b) Evolutionary response of behavior at age 2 to selection imposed on behavior at age 1. Same data as in Figure 9-3a, with the slope of the heavy line reflecting positive genetic covariance. The strength of selection on behavior at age 1 is indicated by the horizontal arrow. The correlated response in behavior at age 2 to selection imposed at age 1 is indicated by the vertical arrow.

Evolution of Behavioral Ontogeny When Selection Acts at a Specific Age

The long-term consequence of genetic correlation is to cause the evolution of temporary maladaptation in the behavioral ontogeny. Imagine a situation in which the environment suddenly changes so that a new behavioral ontogeny is favored by selection. In Figure 9-5 we consider just the initial portion of the behavioral ontogeny, from age 1 to age 2. We suppose that in the old environment the population had evolved an optimal ontogeny (lowest line) but in the new environment there is a new optimal behavioral ontogeny (heavy line), one that slopes downward rather than upward. The only difference between these optimal ontogenies is in the behavioral score at age 1. In the new environment a higher behavioral score is favored at age 1, but the original behavioral score is optimal at age 2 in the old and new environments. Using this simple scenario we can visualize the effects of genetic correlation on the behavioral ontogeny as it evolves under the challenge of a new environment. To construct these visualizations I have used evolutionary theory based on the elementary concept of genetic correlation as well as on the concepts of direct and correlated response to selection (Lande, 1979, 1980).

The population will evolve directly to the new optimal ontogeny in the absence of genetic correlation. In other words, if gene effects are age specific, so that different sets of genes affect behavior at the two ages, the evolution of behavior at age 1 will not affect behavior at age 2. This uncoupled case is illustrated in Figure 9-5. Behavior at age 1 evolves rapidly at first and then slows as it reaches the new optimum, but behavior at age 2 remains at its optimum. Genetic coupling between behavior at the two ages will change this picture of independent evolution.

Genetic correlation will cause behavior at age 2 to evolve temporarily away from its optimum. This effect occurs because genetic correlation causes selection on behavior at age 1 to induce a correlated response in behavior at age 2. If the genetic correlation is positive, as in Figure 9-3a, the ontogeny will evolve in two phases, as shown in Figure 9-6. In the first phase (Figure 9-6a), behavior at age 1 rapidly evolves to higher scores, toward the new optimum. Behavior at age 2 also evolves toward higher scores (at a slower rate than behavior at age 1), away from its optimum. During the second evolutionary phase (Figure 9-6b), behavior at age 1 con-

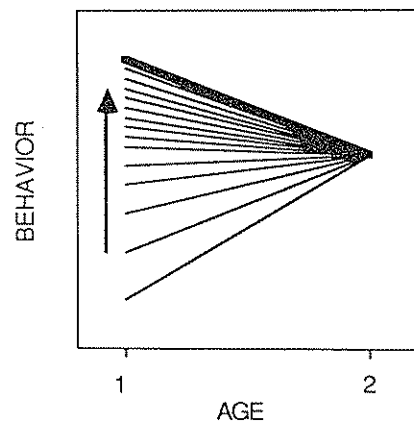


Figure 9-5 Evolution of a simple behavioral ontogeny when there is no genetic correlation between behavior at ages 1 and 2. The ancestral behavioral ontogeny is indicated by the lowermost line. If a new selective regime prevails that favors a markedly increased value for behavior at age 1 but the same behavior at age 2 (heavy line), the behavioral ontogeny will gradually evolve toward that optimum without any change in behavior at age 2.

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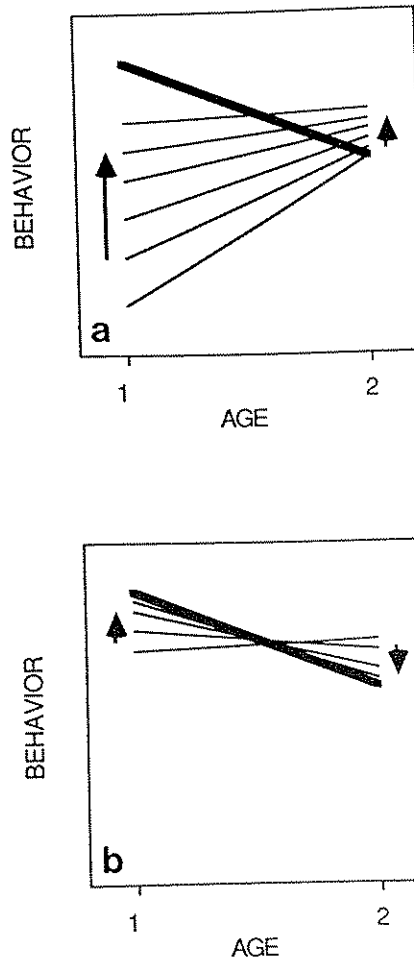


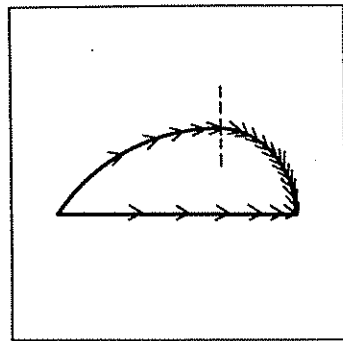
Figure 9-6 Evolution of a simple behavioral ontogeny when there is a strong positive genetic correlation between behavior at ages 1 and 2. As in Figure 9-5, a new selective regime has been imposed so that the new optimum ontogeny is one in which high behavior scores are expressed at age 1 and low scores at age 2 (heavy line). (a) During the first evolutionary phase, behavior at both ages 1 and 2 increases in value. Behavior at age 2 evolves as a correlated response to selection on behavior at age 1. (b) During the second evolutionary phase, behavior at age 1 continues to evolve upward, toward the optimum, and behavior at age 2 evolves downward, toward the optimum.

tinues to evolve upward, decelerating as it reaches its optimum. Behavior at age 2 reverses its evolutionary direction and gradually returns to its optimum.

Another visualization of the two evolutionary phases is shown in Figure 9-7. Here we plot the average ontogeny of the population each generation as a point in a two-dimensional space. The population evolves directly to the new optimum along a straight trajectory in the absence of genetic correlation. Genetic coupling between behaviors at the two ages causes the population to evolve along a curved trajectory. During the initial phase (to the left of the dotted line), the behavior at age 2 evolves away from its optimum, in a maladaptive direction. During the second phase (to the right of the dotted line), behavior at age 2 evolves back toward its optimum.

Selection acting at a specific age can produce evolutionary reverberations along the whole length of the ontogeny. The reverberations will be greatest at ages adjacent to the age(s) at which selection acts. For example, we consider first just the long-term correlated responses of behaviors that are expressed before and after the age that experiences strong directional selection. In Figure 9-8 we consider environmental

AVERAGE BEHAVIOR AT AGE 2



AVERAGE BEHAVIOR AT AGE 1

Figure 9-7 Effect of genetic correlation on evolutionary trajectory. The straight line shows the evolutionary path to a new optimum consisting of a higher behavior score at age 1 and an unchanged score at age 2 when there is no genetic correlation between behaviors at ages 1 and 2. When there is a strong positive genetic correlation, the population evolves toward the new optimum along the curved path. The arrow heads are spaced at approximately equal intervals in number of elapsed generations.

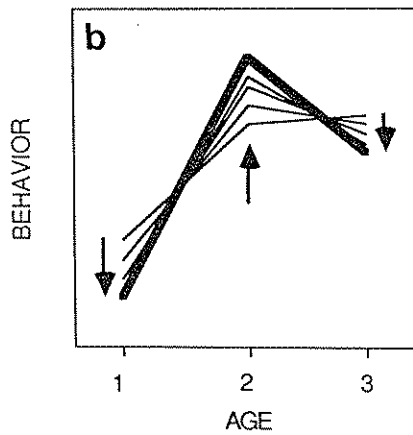
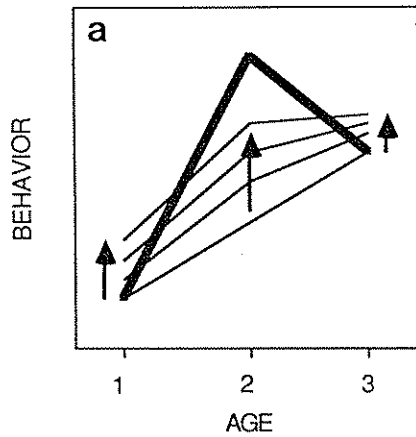


Figure 9-8 Evolution of a behavioral ontogeny toward a new optimum when selection acts directly on behavior only at an intermediate age. The new optimum is indicated by a heavy line and is characterized by the highest behavioral score occurring at an intermediate age. (a) During the first evolutionary phase, behavior at all three ages evolves toward higher scores, with behavior at ages 1 and 2 evolving away from optimal behavior. The ancestral behavioral ontogeny is indicated by the lowermost line. (b) During the final evolutionary phase, behavior at all three ages evolves toward optimal behavior.

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change that favors a new optimal ontogeny. That new optimum differs from the old one only in that high scores are now favored at the intermediate age. The population will evolve directly to the new ontogeny if there is no genetic coupling between behaviors at the three ages. However, the evolution of behavior at the intermediate age will induce evolution of behavior at the other two ages if the behaviors are genetically coupled. Figure 9-8 illustrates the case of positive genetic correlations between behaviors. As before, two evolutionary phases can be recognized: an initial phase of maladaptive evolution by behaviors at the two ends of the ontogeny (Figure 9-8a) and a final phase of approach to the optimum (Figure 9-8b). If we had considered behaviors much earlier and much later than ages 1 and 3, they would have shown less extreme departures from their optima. Maladaptive reverberations would have been less at ages further from the age experiencing selection because of our expectation that genetic correlations will be smaller between behaviors expressed at more disparate ages. The smaller the genetic correlation, the smaller the correlated response to selection (consult Figure 9-3).

In nature an environmental change is unlikely to induce selection at a specific age only. Nevertheless, by focusing on this extreme case we can visualize the consequences of selection pressures that act differently at different ages. As in the extreme case we considered, the evolutionary effect will be to cause temporary maladaptation of the ontogeny.

Genetic Studies of Morphological and Behavioral Ontogeny

Because the morphological literature, while not large, is more extensive than the behavioral, it will be informative for us briefly to review the principal conclusions arising from the morphological studies of ontogeny. First, the heritability of a particular character often varies with the age at which the character is measured. For example, in house mice, the subjects of much of the developmental genetic work, heritability may increase or decrease with age, show a maximum at an intermediate age, or remain roughly constant during ontogeny, depending on the trait (Cheverud, Rutledge, & Atchley, 1983a; Rutledge, Robison, Eisen, & Legates, 1972). Likewise, genetic correlations can change with age and show age profiles that differ from one pair of traits to another (Leamy & Cheverud, 1984; Riska & Atchley, 1985; Riska, Rutledge, & Atchley, 1985).

Second, genetic correlations between morphological traits expressed at different ages are usually highest for traits expressed at adjoining ages. Genetic correlation usually decreases gradually from high positive values as the interval between the two age-specific traits increases (Cheverud, Leamy, Atchley, & Rutledge, 1983b; Leamy & Cheverud, 1984). Likewise, traits that are homologous or contiguous in space often show strong positive correlations among individuals (Bader & Hall, 1960; Berg, 1960; Kurtén, 1953; Lande, 1980b; Olson & Miller, 1958; Pearson, 1903). In all these cases, strong correlations probably reflect pleiotropy (shared gene effects) (Lande, 1980b).

The same trends—heritability changing with age and high genetic correlation between the same trait expressed at adjoining ages—can be seen in the behavioral literature, although the data base is not so large. For example, heritability is constant or increases with age in various behavioral scores for humans (Plomin, 1986; Eaves, Long, & Heath, 1986). Estimates of genetic correlation across ages are scarce because

Over vast stretches of evolutionary time, the genetic parameters themselves will evolve and the supposition of constancy will no longer hold. A current challenge is to determine the time scale over which constancy is likely to hold.

Even without invoking long-term constancy of genetic parameters, we can use the results of developmental studies of morphological and behavioral genetics to predict important short-term consequences (e.g., Cheverud et al., 1983a). Thus the result that a particular behavior is likely to show a high genetic correlation when expressed at adjacent ages has immediate evolutionary consequences. To visualize those consequences, it will be helpful to consider some behavioral examples.

PROSPECTS FOR ANALYZING THE INHERITANCE AND EVOLUTION OF BEHAVIORAL ONTOGENIES

Ontogenetic change in the niche, alternative male mating tactics, and bird song share several common denominators that make these behaviors particularly promising subjects for genetic analysis. First, the ecological setting for all three types of behavior is well understood, so that the actual agents of selection are accessible to the investigator. Often when behaviors are studied only in the laboratory, the selection pressures confronting the population in nature are unknown or only dimly perceived. Without an ecological reference, the investigation can easily drift away from substantive evolutionary issues. Second, in each case comparative studies have revealed the aspects of behavior that are most prone to evolutionary change. By comparing songs in different bird species, for example, we can determine which aspects of song are most variable among species and so identify the aspects most liable to evolutionary modification. Such a diagnosis can be used to focus genetic studies on recurrent evolutionary themes. Third, all three types of behavior have a strong developmental dimension. Patterns of resource use, mating tactics, and bird song can all show pronounced change during ontogeny. Perhaps because of this developmental complexity, these behaviors share the fourth characteristic: virtual absence of genetic analysis. The developmental dimension seems to have thwarted even the first stage of conceptualizing the relevant genetic issues. The literature on each of these three topics has often bogged down in the retrogressive pattern of treating ontogenetic modification and inheritance as alternatives. How can we move forward?

Evolution of Ontogenetic Shifts in the Niche

Werner and Gilliam (1984) emphasized the point that the ecological niche has an ontogenetic dimension and stressed its importance for population dynamics and species interactions. Very commonly the pattern of resource utilization changes with age and size, so that juveniles exploit different foods and face different hazards and competitors than do adults. Many fish, for example, progress through several abrupt shifts in diet during ontogeny. To illustrate the genetic phenomena that may play a role in the evolution of such niche shifts, I will focus on a simpler example, the striped swamp snake.

The striped swamp snake (*Regina alleni*) is a small, aquatic natricine snake commonly residing in the floating water hyacinths found in Florida and southern Geor-

gia. Juveniles feed predominantly on the aquatic larvae (naiads) of damselflies, but adults shift over to a diet of recently molted, soft crayfish (Godley, 1980). The dietary shift is accompanied by a change in prey-handling behavior. Crayfish are swallowed tail first but damselfly naiads are swallowed head first (Franz, 1977; Godley, 1980).

Comparative studies suggest that damselfly feeding is a more recent evolutionary innovation than crayfish feeding. The ancestral *Regina* was undoubtedly a crayfish feeder, since all four extant species in the genus have this habit (Rossman, 1963) and no other North American natricine snake regularly feeds on these prey. *R. alleni* is the only species in the genus that also preys on damselflies. A secondary addition of damselflies to the diet is also suggested by the fact that both juvenile and adult *R. alleni* will readily feed on crayfish in the laboratory. Godley (1980) suggested that the feeding propensities of juveniles are broad, so that the diet varies with seasonal availability of prey. Small crayfish are rare during the seasons when *R. alleni* juveniles are growing to maturity, but damselfly naiads are common.

The ontogenetic diet shift in *R. alleni* may reflect an ontogenetic change in chemoreceptive response to prey. In other species of *Regina*, naive newborn snakes give an active tongue-flicking response to crayfish odors but not to prey that do not occur in the diet (Burghardt, 1968). The flicking tongue transports odiferous particles to a chemosensor, the Jacobson's organ, in the roof of the mouth (Burghardt & Pruitt, 1975). The ontogeny of chemoreceptive responses to prey have not been studied in *R. alleni* or in any other *Regina*, but the ontogenetic dimension has been studied in a related natricine snake. The red-bellied water snake (*Nerodia erythrogaster*) shifts from a juvenile diet of fish to an adult diet of frogs (Mushinsky, Hebrand & Vodopich, 1982). This snake shows no ontogenetic change in chemoreceptive response to fish, but chemoreceptive response to frog odor increases suddenly as snakes reach maturity. Remarkably, the ontogenetic patterns for responses to fish and frog odor were unaffected by rearing snakes on fish versus frogs (Mushinsky & Lotz, 1980).

In other natricine snakes, populations show heritable variation in the chemoreceptive prey responses of naive juveniles. Unfortunately no genetic studies have been conducted with *Regina* or *Nerodia*. In related garter snakes (*Thamnophis*), analyses of full-sib families have revealed heritable variation in responses to the odors of a number of different prey (Arnold, 1981a,b). Those studies suggest that the chemoreceptive responses can respond to selection, and indeed, population differences in chemoreceptive response correspond to population differences in diet (Arnold, 1981a).

Returning to our damselfly-eating *Regina*, for which phylogenetic inferences are the strongest, we can try to view evolution of the ontogenetic niche from a genetic perspective. Selection for juvenile predation on damselflies in the ancestral crayfish-eating population of *R. alleni* may have produced a maladaptive evolutionary phase characterized by increased adult predation on damselflies. If, for the sake of concrete discussion, we take chemoreceptive response to damselflies as a possible target for selection, then we imagine selection favoring increased juvenile responsiveness to damselflies, but no corresponding selection on adults (juveniles but not adults are faced with a food shortage). If juvenile responsiveness were genetically coupled to adult responsiveness, as seems possible, adults would experience a correlated response to selection as juveniles. Over a period of many generations, adult response

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to damselflies would increase and then decrease, as ontogenetic differentiation in chemoreceptive response was gradually achieved (see Figure 9-6).

This example of genetic influence on the evolution of niche ontogeny is necessarily hypothetical because critical ontogenetic and genetic information is missing. Nevertheless, a quantitative genetic perspective raises issues not previously addressed in the ecological literature. Furthermore, by making geographic comparisons within *R. alleni* we might catch populations still engaged in the final slow stages of ontogenetic differentiation and so test the prediction of temporary maladaptation.

Evolution of Alternative Male Mating Tactics

In a wide variety of animals, males use two or more tactics to gain mating success (Austad & Howard, 1984; Dunbar, 1985). Often these alternative tactics represent a contrast between offensive and defensive maneuvers in male-male competition for mates (Arnold, 1976). For example, the primary tactic may be to guard the female from rivals, while a secondary, offensive tactic may be to steal the female away from another guarding male. Alternatives such as these may involve polymorphism (in which males show persistent individual differences in behavior), facultative shifts in tactics (tactics vary with circumstances), and ontogenetic change in tactics. These are not mutually exclusive; in some of the most thorough studies, polymorphism, facultative shifts, and ontogeny change occur in the same population. Here I will focus on one such case, North American bass and sunfish. Caro and Bateson (1986) have recently emphasized the ontogenetic dimension of alternative tactics. I hope to extend their discussion by concentrating on the genetic issues.

Comparative studies by Gross and his colleagues highlight some behavioral transitions that must have occurred during the evolution of mating systems in North American sunfish and their relatives (Figure 9-9). Rock bass (*Ambloplites rupestris*) males use only a single mating tactic (Gross & Nowell, 1980). They build shallow cuplike nests in the shallow water along lake margins and defend them. Females visit these nests, spawn, and immediately depart. Males tend the eggs until they hatch and defend them against predators and egg-eating conspecifics.

Pumpkinseed sunfish (*Lepomis gibbosus*) males facultatively shift between two tactics, and employment also varies with age (Gross, 1982). Larger, older males build and defend nests, as do rock bass, but they will also sneak into the nests of a male in an adjoining territory while that male attempts to spawn with a female. The sneaking male releases sperm over the spawning couple, fertilizing some of the eggs. The sneaker immediately returns to his territory and the rival rears his offspring. Younger, smaller males use the sneaking tactic. Perhaps they also use the nest-building parental tactic on rare occasions when nest sites are available.

The mating system of male bluegill sunfish (*Lepomis macrochirus*) consists of two ontogenetic pathways as well as facultative shifts in tactics (Gross, 1982). Some males mature relatively late in life. These large males adopt the parental nest-building tactic at about 7 years of age and use it consistently for three or four years, until they die. These parental males will also use the sneaking tactic on occasion when a rival is spawning in an adjoining territory. Other males in the bluegill population mature at an earlier age. These smaller males reach sexual maturity at 2 years of age and adopt

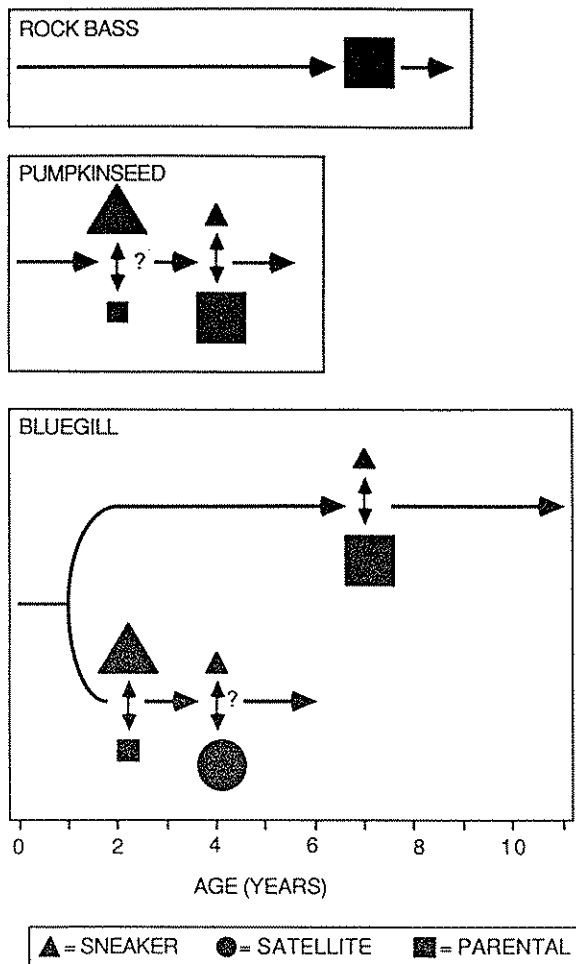


Figure 9-9 Ontogeny of alternative male mating tactics in rock bass, pumpkinseed sunfish, and bluegill.

sneaking as their primary tactic. The tactic is facultative, for these small, young males will build and defend nests when population density is low and nest sites are available. Later, at the age of 4 years, the small males have grown to the size of mature females and adopt a new, so-called satellite mating tactic. Satellite males defend territories in mid-water above the territories of the larger, parental males. Satellite males do not build nests. Instead, they slowly move into the nests of spawning, parental males and steal fertilizations. Facultative shifts between sneaking and satellite tactics have been observed in males that grow along this second ontogenetic pathway have been observed.

In summary, four kinds of evolutionary change are needed to account for the differences among just these three centrarchid species. For the sake of concrete discussion, I will consider the mating system of the bluegill to be the most derived. One could equally well consider the following changes as occurring in the opposite direc-

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tion (e.g., such a system would be needed to account for the evolution of alternative ontogenetic pathways of ontogeny of alternative tactics we can see in nature).

Consider the ontogeny of alternative tactics in bluegill. The ontogeny of alternative tactics is much less complex than that of alternative tactics in rock bass. In bluegill, the young are exposed to a wide range of stimuli. In bluegill, the expression of alternative tactics can be anticipated through evolutionary changes in critical genes. Genes expressed at an early age would expect to be time-consuming.

The evolution of alternative tactics in bluegill is some additional complexity. The bifurcation of alternative tactics in bluegill is a result of alternative inheritance and polymorphism. It is unlikely that alternative tactics in bluegill are instantaneous. Instantaneous alternative tactics in bluegill are a result of ontogeny of alternative tactics in bluegill. This scenario is related to the bifurcation of alternative tactics in bluegill.

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Comparative studies of alternative tactics among species may be over 100 species in the marsh warblers of bluegill (Dowsett-Jones).

tion (e.g., substituting loss of tactics for gain of tactics). Additional comparative work would be needed to settle the issue of evolutionary polarity; the present discussion relies only on the necessity of change that is implied by the species differences. The needed transitions are (1) evolution of an earlier onset of sexual maturity, (2) evolution of a facultative shift to new tactics (sneaking, satellite behavior), (3) evolution of ontogenetic changes in facultative shifts between tactics, and (4) bifurcation in the ontogeny of behavior and morphology. By focusing on these elements of evolution, we can see some of the genetic issues.

Consider, for example, the evolution of a new mating tactic, sneaking. In one of the ontogenetic pathways in bluegill, the tactic is expressed in young males, and to a much lesser extent in older males. It is conceivable that older males are simply not exposed to the environmental circumstances that elicit sneaking. It is also possible that young males are more prone to sneak than older males, given the same eliciting stimuli. In this case we must consider the evolution of age-specific differences in the expression of sneaking. From our preceding discussion of genetic correlation, we can anticipate that selection for sneaking in young males would have caused a correlated evolutionary response in older males as well as in the young targets of selection. The critical genetic parameter giving the effect is a genetic correlation between sneaking expressed at early and later ages. Following our earlier theoretical discussion we would expect the elaboration of age-specific differences in behavior to have been a time-consuming process perhaps lasting many thousands of generations.

The evolution of the bifurcation in ontogeny seen in bluegills probably involved some additional genetic phenomena. Let us explore, for example, the possibility that the bifurcation represents a genetic polymorphism. In the simplest case, the inheritance of alternative ontogenies could behave as simple Mendelian inheritance. Such inheritance is known for many polymorphisms, including the primary sex differences and polymorphisms involving coloration in many organisms. In such cases it is unlikely that the polymorphism evolves by saltation, with mutation to a gene that instantaneously produces all the differences associated with the present-day dimorphism. Instead, the polymorphism is probably built up gradually by selection for numerous genes that modify and augment the effects of a gene that acts as a developmental switch (Fisher, 1958, pp. 181-185). A good working hypothesis for the bluegill case is that the bifurcation was gradually elaborated from some ancestral ontogeny so that the present dimorphism behaves as a Mendelian factor. Under this scenario we would predict that populations of bluegill, as well as closely related species, might show variations in the completeness of developmental bifurcation.

Inheritance and the Evolution of Birdsong

Comparative studies of birdsong have revealed tremendous variation in repertoire size among species (Krebs & Kroodsma, 1980; Marler, 1981). Individuals in some species may sing a single type of song, whereas individuals of other species may sing over 100 different songs. At one extreme, the average repertoire of an individual marsh warbler (*Acrocephalus palustris*) includes imitations of songs from many species of birds; the species as a whole is known to imitate the songs of 212 other species (Dowsett-Lemaire, 1979). Differences in age-specific tendency to incorporate new

songs into the repertoire are an important component of species variation in repertoire size. Some species learn songs only during a critical period, whereas other species add songs to their repertoire throughout life.

Two lines of evidence indicate that repertoire size affects male mating success (Krebs & Kroodsma, 1980). In red-winged blackbirds (*Agelaius phoeniceus*), males with larger repertoires have larger harems of females, but the correlation is apparently due to common correlation age (Yasukawa, Blank, & Patterson, 1980). In mockingbirds (*Mimus polyglottos*), males with larger repertoires breed earlier in the year, although the effect may be due to common correlation with territory quality (Howard, 1974). In the best study of fitness effects, McGregor, Krebs, and Perrins (1981) found that great tits (*Parus major*) with intermediate repertoire sizes left the most descendants. In this species repertoire size does not change with age. Kroodsma (1976), in an experimental study with canaries, found that repertoire size affected female nest building. While some of these results are equivocal, it seems likely that sexual selection exerted by mate choice has been an important force in producing diversification of repertoire size.

Comparative and experimental studies have identified onset and length of a sensitive learning period, tendency to incorporate songs into the repertoire during the sensitive period, and the size of the pool of tutors as key variables in the ontogeny and diversification of repertoires (Marler, 1981). Auditory input and feedback are critical for song development.

Males deafened early in life produce only the rudimentary elements of song, and birds deprived of tutors or model songs develop only simplified versions of species-characteristic songs. In some species songs are learned during a sensitive period lasting only a few weeks, but in others incorporation of new songs continues throughout life. The bird is not a *tabula rasa* during the sensitive period. Many song birds, for example, selectively learn the songs of conspecifics and reject the songs of even closely related species. Finally, the timing of the sensitive period in relation to dispersal can greatly affect the adult's repertoire size. The males of some species learn songs from their fathers. In other species the sensitive period does not begin until after the young male has left his natal territory. In such species the male may be exposed to a large pool of different conspecific songs.

To understand how repertoire size evolves, we need genetic studies of the developmental and learning processes. To date only one genetic study has focused on the key issues, and that study gave an unexpected result. McGregor et al. (1981) were unable to detect any father-son resemblance in the repertoire sizes of great tits. Is this an anomalous result (the sample size was small) or is there typically a low or even zero father-son resemblance in repertoire size? It may be that song characteristics are transmitted from one generation to the next by cultural channels that do not involve lines of descent. McGregor et al.'s (1981) results notwithstanding, let us consider some different models of transmission that could produce father-son resemblance in repertoire size, to see the genetic issues more clearly (Figure 9-10).

A nongenetic conception of song and repertoire transmission is implicit in much of the bird-song literature. Two varieties of this idea are shown in Figure 9-10. In the first model, sons do not learn songs from their fathers. Nevertheless sons resemble their fathers because they inherit or take over the father's territory and are conse-

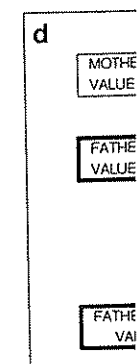
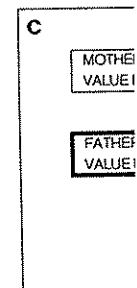
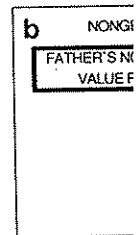
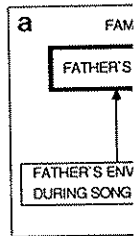


Figure 9-10. Models of transmission indicated by arrows.

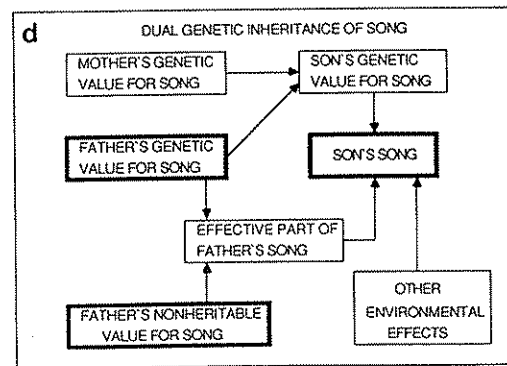
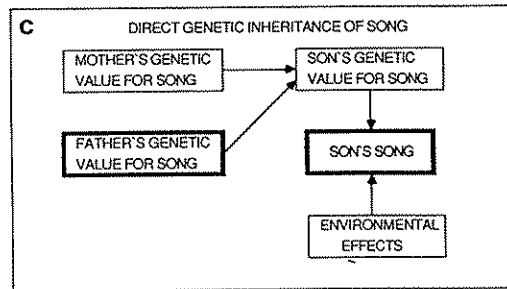
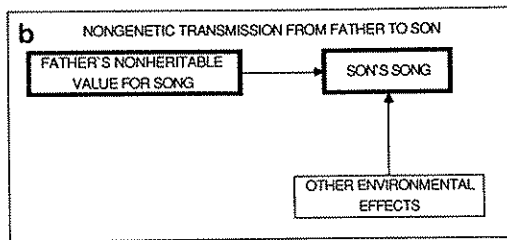
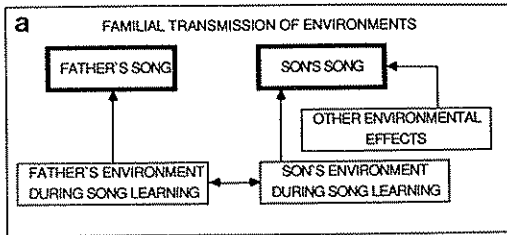


Figure 9-10 Four models for father-son resemblance in songbirds. Causal paths are indicated by single-headed arrows. Correlations are indicated by double-headed arrows.

quently exposed to a common set of tutors (Figure 9-10a). Alternatively, sons might resemble their fathers because they learn their father's songs (Figure 9-10b). As before, the transmission of songs and repertoire is nongenetic. Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) have modeled and discussed these and other modes of purely cultural transmission.

Genetic transmission of songs is both conceivable and compatible with song learning. For example, the son might inherit a genetic propensity to sing a particular song or to develop a large repertoire. (Such genetic propensities could be transmitted both by fathers, who express the tendencies, and by mothers, who do not. Many sex-limited traits are affected by autosomal genes). Genetic transmission could promote father-son resemblance even though sons do not learn their fathers' songs and instead use unrelated tutors (Figure 9-10c).

Finally, father-son resemblance in repertoire could arise from dual inheritance in which the son inherits his father's propensities and also learns the father's songs. Models of dual inheritance have been used by quantitative geneticists for many years to analyze maternally affected traits in mammals (e.g., offspring body size) (Cheverud, 1984; Dickerson, 1947; Riska et al., 1985; Willham, 1963). A simplified version of the scheme is shown in Figure 9-10d. The key feature in this model is that the aspects of the father's song that are effective in teaching the son may themselves be heritable. Consequently father-son resemblance arises from two genetic routes: direct genetic effects on singing propensities and the genetic part of the father's singing.

Controlled breeding and manipulative experiments will be needed to distinguish between these and other models of song transmission. For example, cross-fostering could be used to determine whether tutoring by the father augments father-son resemblance. To cleanly estimate the many genetic parameters in the dual-inheritance model one needs a correspondingly large number of different kinds of relatives (e.g., paternal half sibs, full sibs, double first cousins, etc.) (Eisen, 1967; Willham, 1963) or a combination breeding and cross-fostering design (Atchley, Plummer, & Riska, 1985, Table 2). For example, it would be particularly useful to have many sets of paternal half-sib brothers and to know their song characteristics and those of their sons.

Correlation between direct and paternal genetic effects in the dual-inheritance model is of particular evolutionary interest. The important postulate of that model is that an individual's phenotypic value for song includes two genetic parts. One part acts directly in the individual, perhaps by affecting that individual's responsiveness to particular song types. The other part acts through the paternal song tutor. This paternal genetic part of song will influence the tutoring effect of the individual's song upon his sons. A particular gene may have effects on both of these genetic parts of song phenotype. The aggregate effect of many such pleiotropic genes can be to produce a genetic coupling or correlation between the two parts of song. The resulting genetic correlation might be positive or negative. If the correlation is positive, selection favoring high values for one or the other part of song will augment the evolution of the other part. But if the correlation is negative, evolution may be counter-intuitive (Cheverud, 1984; Dickerson, 1947). Selection for high values of one part of song could override selection for high values of another part and cause that part to evolve toward lower values. Thus, selection acting on the tutoring aspect of song could interfere with the evolution of the student part of song learning.

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Ontogeny is a dimension of the phenotype and genotype rather than an alternative to inheritance. To confront the key issues of how behavioral ontogenies are inherited and how they evolve, it is essential to see inheritance and ontogeny as complementary phenomena rather than as alternative explanations.

Quantitative genetics is a natural tool for analyzing the inheritance of behavioral ontogenies. The analytic machinery of this discipline is designed to deal with traits whose genetic variation is affected by many genes of individually small effect. Such genetic variation is common for morphological traits and probably for behaviors as well. In addition, a tradition of genetic analysis of morphological ontogenies provides a series of useful conceptual guideposts for the behaviorist. For example, the simple step of defining age-specific behaviors can make the ontogenetic dimension manageable.

Another important lesson from morphological studies is that longitudinal data are crucially important. Selection acting on ontogeny works on individual variation in ontogenetic trajectories, so it is crucial to describe that variation in order to understand selection. From a genetic standpoint one cannot compute genetic covariances between behaviors expressed at different ages unless individuals or families are followed through time and their behaviors scored at regular intervals.

To make incisive evolutionary studies of behavioral ontogeny, the feasibility of ecological work is as important as the feasibility of genetic analysis. An important criterion for genetic work is that individuals of known relationship can be identified in the field or bred in the laboratory. To test evolutionary hypotheses, we have the additional criterion that the behavior and its ontogenetic dimension can be placed in an ecological context. At a minimum we need observations that suggest how the behavior functions in a natural context. Ideally, we want careful demographic work that enables us to evaluate the fitness consequences of behavioral and ontogenetic variation. Thus an ideal behavior is one that can be observed in the field, is performed by an organism amenable to genetic work, and occurs in populations in which selection pressures can be directly measured.

Comparative studies can be of critical importance in identifying which aspects of behavioral ontogeny are most prone to evolutionary modification. Of the examples explored in this chapter, we have by far the best grasp of important evolutionary issues in the case of birdsong. Here the evolutionary issues are apparent because of in-depth studies of developmental processes and an abundance of comparative studies. From these two sources, length of the sensitive period for song learning emerges as a key variable, one that is particularly prone to evolution. In the cases of niche ontogeny and alternative mating tactics, the identification of key variables is more speculative because comparative studies of behavioral ontogeny are rare.

Genetic studies of facultative shifts in behavior are greatly needed. Behavioral shifts are particularly evident in studies of alternative mating tactics. Particular males commonly change their mating tactics according to circumstances: guarding their mate when another male intrudes, playing the role of intruder when they themselves are not guarding. By slowly changing the probabilities of using one or the other tactic under particular circumstances, we could easily model the evolution of complex sys-

terms of tactics. Unfortunately, we lack concrete data on the inheritance of facultative shifts. As a first step we need to know whether there is phenotypic variation in the parameters of behavioral plasticity in natural populations.

Genetic correlations are of crucial importance to the evolution of behavioral ontogenies, and yet they are seldom discussed outside the quantitative genetic literature. The importance of heritability for evolution is now routinely acknowledged outside the technical literature, some 50 years after the concept was first employed in animal breeding (Lush, 1937). The importance of genetic correlations was first stressed by Hazel in 1943, and such correlations have been employed ever since in schemes maximizing gains from deliberate selection on domesticated species (Falconer, 1981). The evolutionary importance of genetic correlations has recently been explored by Lande in a series of papers (Lande, 1979, 1980a, 1981, 1982; Via & Lande, 1985). Despite this long history of application and the recent surge in evolutionary inquiry, behaviorists and psychologists have tended to overlook the importance of genetic correlation. The first estimates of genetic correlations for behavioral traits were published only within the last two decades (DeFries & Hegmann, 1970; Hegmann & DeFries, 1970a,b; Henderson, 1972).

The present review has revealed two general situations in which genetic correlations are likely to play an important role in behavioral evolution. First, genetic correlation between the same behavior expressed at different ages is likely to impede the evolution of age-specific behaviors. Such correlations are likely to slow both the process of ontogenetic differentiation of the niche and the elaboration of ontogenetic differences in male mating tactics, for example. Second, in systems of dual inheritance, genetic correlation between direct effects on behavior and effects mediated through learning can cause counterintuitive evolutionary effects. A dual system of inheritance is conceivable for singing in birds and in many other behavior circumstances, and yet formal behavior genetic tests of the model have not been attempted. These two situations are examples of the general rule that genetic correlations cause curved evolutionary trajectories and promote temporary maladaptation (Lande, 1980a).

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