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BEHAVIORAL ENVIRONMENTS AND EVOLUTIONARY CHANGE

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INTRODUCTION

Phenotypes of organisms are produced by complex interactions between genetic and environmental information (112, 165, 218, 227). Beginning with Darwin (49) biologists have generally neglected the evolutionary importance of phenotypic modifications, largely due to Weismann's cogent arguments that there is a separation, early in ontogeny, between germ- and somatic-cell lineages in many taxa (see 35). This review focuses on the origins of novel behavior and emphasizes the importance of phenotypic modifications in evolution. Numerous comparative examples are given which suggest that behavioral change usually precedes external morphological evolution. Individual phenotypic modifications influence subsequent genetic evolution, not by direct somatogenic induction of acquired characters (see 179), but by partially determining demographic and selective factors at a higher level of biological organization (see 135, 238, 239a for macro-evolutionary consequences).

Behavioral characters are sometimes useful in reconstructing phylogenies, as is shown by Lorenz and others (e.g. 56, 67, 128, 129, 134, 140, 145, 233). Schmalhausen (190) discussed how these same "historically-determined" patterns of behavior are also part of the process of evolution, altering the effects of natural selection and other evolutionary processes at the population level. A behaving "*organism*" represents the only entity recognized in both an ecological and a genealogical hierarchy of evolutionary "individuals" (63).

Schmalhausen emphasized that the behavior of animals, though genetically specified, can only be understood in terms of the interaction with the "environment" during development (i.e. the reaction norm—81, 125). As a result, the organisms' hereditary behavior modifies the physical and social

environment during the interaction (15, 125, 163). Many examples of human behavior show how schemes of artificial selection have profoundly influenced evolutionary change in domesticated plants and animals, and in their pests (20, 41, 85, 175).

The relative importance of the interactions in altering selection coefficients depends in part on the complexity of the behavior and is probably most pronounced for learned behavior. Wright (250: p. 143 ff.) gave a table of 17 factors influencing evolution, listing them as pairs in two columns according to their tendency to increase a species' genetic homogeneity or its heterogeneity. In the nine diametrical pairs "individual adaptability" is listed twice, once acting to increase homogeneity and once increasing heterogeneity. Wright thought that individual adaptability "is itself perhaps the chief object of selection." West-Eberhard (238, 239a—this volume) discussed how individual adaptability ("alternative phenotypes") potentially facilitates speciation.

The principal (nonexclusive) hypotheses that emphasize the feedback relationships between modifications in animals' behavior and subsequent evolution are briefly given as follows (modified from 15). Each hypothesis is discussed below.

1. Inherited capacities to learn enable animals to exploit novel situations (generated by Nos. 2–5, below) in which resources would be otherwise inaccessible. In its simplest form, this means individuals survive and reproduce rather than die. In its most developed form, when accompanied by imitation and teaching, learning is especially important because it allows rapid horizontal transmission of a novel behavior throughout a population.

2. Animals with parental behavior change the physical and social environments in which their progeny develop. These alterations therefore affect subsequent evolutionary processes (selection, drift, etc).

3. Behavioral "invasion" of a novel environment by adults exposes the tail ends of the reaction norms of their progeny. This reveals genetic variability never expressed in the original environment.

4. Behavioral flexibility enables animals to compensate for changes in structure, physiology, etc, generated by changes at the genomic level (e.g. due to mutation, molecular drive).

5. Many behavioral traits develop later in ontogeny relative to structural traits. Due to this temporal relationship, any alterations in developmental pathways that produce structure influence what behavior is expressed (e.g. size-dependent alternative mating tactics, 220, 237). Alterations in pathways producing behavior influence what structures are viable at the population level.

In a monograph on sand wasps (Bembicinae) Evans (68: p.2) noted that "one cannot intelligently discuss behavior and structure separately. Behavior

is what an animal does with its structure; structure is what an animal uses to behave." Nonetheless, to the extent that behavioral and structural characters are expressed independently (low covariances) they will evolve independently (225, 238). To what degree is behavioral evolution coupled with external structural evolution, and vice versa? There are parasitic wasps and aquatic moths, for example, that swim underwater but show little or no external morphological change at the macroscopic level (42, 91, 120). [Structural changes at the neurological level will not be treated in this review (see 178).] Many morphologically monotonous sibling species have been first recognized on ethological bases, and then later structural differences were found (e.g. 134, 136). Numerous apparently "functionless" structural differences between species with similar behavior are well-known to taxonomists (182); more detailed study may reveal previously unknown functional differences (see e.g. 58).

Somatic changes in individuals alter the context in which populations are evolving; for populations to respond genetically is a *non-necessity* (see 10). *All* categories of phenotypic characters (physiology, behavior, structure, etc) influence evolutionary change and are themselves products of evolution. The relative importance of the feedback linkages between each category and evolutionary change in the others is empirically unknown. This review focuses on behavioral phenotypes and is principally intended to state explicitly some frequently asserted hypotheses. Two other recent reviews (15, 171) discuss behavior and evolution in vertebrates. Many examples in this review, therefore, are taken from invertebrates, mostly Arthropoda, to underscore the potential generality of the hypotheses.

HISTORICAL REVIEW

The role of behavior in evolution has been repeatedly discussed, and historical perceptions seem to have influenced subsequent thinking. To avoid certain misinterpretations, a brief review of earlier contributions follows.

Lamarck

Perhaps as a consequence of widespread misconceptions about what Lamarck (119) wrote, biologists appear to suffer from "bath-waterism" (69—i.e. throwing out the good with the bad) when they think of Lamarck's biological contributions. Diverse authors have pointed out that Lamarck was correct in emphasizing that behavior is somehow important in changing form (125, 138, 182). Lamarck never suggested a plausible process, although he *explicitly* (119: p. 107) rejected direct somatic induction of characters from the environment (see 138).

Darwin's Views and His Legacy

Darwin's main interest in behavior was to show that various historical patterns, even extreme, potentially "fatal" examples (e.g. social sterility, parasitism), could be explained by his theory of evolution (49–52). He was noncommittal on the question of the role of behavior in evolutionary processes (49: p. 183).

Darwin's great contributions in explaining patterns of evolution were possible in part because he was able to separate *conceptually* "the organism" from "the environment." To express this idea, he used a literary device and personified natural selection (from 45), e.g.,

It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working . . . (49: p. 84).

Darwin knew he was writing metaphorically, yet this literary device is so useful that we sometimes assume that natural selection is an external agent acting on *passive* organisms. It is a view of the environment as a static lock, and natural selection as a locksmith cutting (adapting) animals as keys to fit these rigid locks (30). Corning (45) cited passages in books by Mayr, Simpson, and Dobzhansky showing that they too adopted this shorthand (but he did not mention they recognized it as such). He argued that this has influenced ways in which many evolutionists view natural selection (also 15, 66, 125, 138).

The Views of Baldwin, Osborn, and Morgan

At the turn of the last century Osborn (164), Morgan (156), and Baldwin (8) published a series of works in which they developed a hypothesis to explain the origins of adaptation. These authors recognized that many animals are not passive, and they stressed the role of individual phenotypic accommodation¹ in their hypothesis. They postulated that organisms may persist in an ecological niche solely because of behavioral adaptability and other nonheritable modifications. Subsequently, any genetic mutations for phenotypic changes (structural, behavioral, etc) suitable to the novel mode of life will have a better chance of being selected. Baldwin et al termed this process "organic selection."

The hypothesis of Baldwin et al implies that natural selection may favor a broader or narrower norm of reaction, assuming the "breadth" of the reaction norm is under genetic control. This hypothesis requires three conditions, and examples illustrating each are given below: (a) The genetically-specified

¹A term implying facultative expression of a trait.

developmental systems of individuals enable the expression of phenotypic traits which enhance survival under certain conditions. The phenotypic modifications themselves are never directly heritable, only the genetic information needed to produce them. (b) At the population level there is genetic variability among individuals in the degree to which modifications develop, due to genomic processes (e.g. mutation). (c) Natural selection may favor those individuals with *more or less* capacity to express specific traits under appropriate conditions.

From the "Modern Synthesis" to "Sociobiology"

Huxley (106) drew the attention of the modern synthesizers to the "unduly neglected" feedback relationships between behavior and evolution (also 105). Pronouncements by leading evolutionists showed their unanimity on the evolutionary importance of individually flexible behavior. Despite this agreement, there has been little theoretical analysis and even less experimental work to test the hypothesized relationships.

THE SYNTHETIC VIEW Simpson (202) reviewed "organic selection," but christened the hypothesis "the Baldwin effect." He concluded that it was mechanistically plausible, although probably of minor importance in evolution. He correctly noted that Huxley was not critical in accepting data that purportedly support the thesis of Baldwin et al. Gause (81, 82) discussed a similar hypothesis and also presented experimental data on reaction norms in clonal organisms that he thought supported his views (see 201 for criticisms). Simpson (202) argued that many of the examples supposedly explicable by "the Baldwin effect" were open to the criticism "that when the characters in question are demonstrated to be hereditary, there is no evidence whatsoever that they had occurred as accommodations before they became hereditary" (p. 113). Examples are discussed below to address these criticisms.

Simpson (203) later altered his opinion that modifications in behavior were of minor evolutionary significance. He stated:

An aspect of the synthetic theory especially pertinent here is that it . . . not only points the way to evolutionary, historical explanations of existing behavior patterns but also involves behavior as one of the factors that produce or guide evolution. (p. 21)

Hardy (95) also reviewed earlier work. He believed Waddington's model of "genetic assimilation" provided a genetic mechanism for Baldwin's hypothesis. Waddington (*in litt.* to Hardy, see 227) disagreed because of an imprecise description (e.g. 134: p. 354) of Baldwin's hypothesis as a "non-genetic" plasticity of the phenotype that influences subsequent genetic change. The degree of plasticity of the phenotype itself has a genetic basis if the system is to evolve.

MAYR'S CRITICISMS OF "THE BALDWIN EFFECT" Mayr (134–139) repeatedly emphasized the role of behavior, especially in his insightful discussion of the origin of evolutionary novelties. Most recently, he reiterated his view that "almost invariably, a change in behavior is the crucial factor initiating evolutionary innovation" (139). In earlier work, however, Mayr (136: p. 611) was critical of "the Baldwin effect" (*sensu* 202) and suggested it was "desirable to discard this concept altogether" because of "three assumptions" which he deemed "fatal to the hypothesis:"

1. "The argument is always stated in terms of the individual genotype" [i.e. the argument is typological].
2. "It is not nearly as strongly emphasized (as is important for the correct interpretation) that the degree of modification of the phenotype is itself genetically controlled."
3. "The Baldwin effect makes the tacit assumption that phenotypic rigidity is selectively superior to phenotypic flexibility."

A proper understanding of these points is essential. Populations evolve, not individuals (136), and Morgan's step No. 8 (see Appendix) shows that Baldwin et al were thinking in terms of *populations* ("a group of organisms"). Mayr's second point is also important, but it is not a valid criticism since their hypothesis required (No. 9) that there be genetic ("innate") variability in plasticity. Lastly, Morgan's No. 18 shows that these authors did not make the third assumption Mayr ascribed to them; in fact, they apparently perceived the benefits of flexible alternative phenotypes and suggested that selection acts to restore some flexibility following the fixation of a new trait (see 68, 210, 238).

DEVELOPMENTAL SYSTEMS Early embryologists (e.g. Dohrn & Roux, see 184) described pattern formation in a hierarchical way. Findings from recent studies of morphogenesis generally support a hierarchical view (112, 218). Within a life history stage, as ontogeny proceeds, the influence of the external "environment" becomes progressively more important in determining form and function. Dohrn's proposed mechanism of "function-change" was applied to behavior by Schrödinger (199) and Popper (174). Schrödinger suggested that chance genetic variations in an organ occur, and those individuals with the behavior to use the novel form in an advantageous way are more likely to survive and reproduce. Popper was more direct, postulating that a developmental monster (*sensu* 83) might render itself "hopeful" by behaving in ways appropriate to the monstrosity (e.g. 173).

Based on empirical studies Waddington (227) repeatedly emphasized that developmental systems are to some degree modified by the environment while

to some degree they resist modification. The balance corresponds to the degree of "canalization" (buffering) and is itself a genetic trait (see 227, 228). Schmalhausen (190) and colleagues (refs. in 81, 82) also discussed this same historical tension during morphogenesis between genetically specified tendencies to resist change and to be modified.

THE ONTOGENY OF BEHAVIOR

Ontogeny is usually thought to be evolutionarily important because it historically "constrains" the realization of certain developmental pathways (205, 218). An additional way to incorporate individual developmental phenomena into evolution is by recognizing that evolutionary processes at the population level are focused in a direction partly determined by phenotypic patterns of individuals arising during ontogeny (also 211).

Based on present knowledge, morphologic traits determined later in ontogeny tend to be more variable than those determined earlier (35, 183, 218). It is well known that structural traits of juveniles are often less derived relative to adults (25, 87, 205, 218). In ontogeny, any "new" structures are built into preexisting structures. This same relationship holds for certain kinds of behavior, such as those due strictly to changes in neural maturation (without practice), or behavior involving constructs (57, 233). Extending this reasoning, those behavioral traits determined later in ontogeny should display more developmental plasticity than those determined earlier in ontogeny (26). For other behavior there seem to be no a priori reasons why a developing behavior must incorporate an already determined behavior (12, 13, 170). Elements or units of behavior are reordered over evolutionary time, as is shown by examples of ritualization or nest construction (below).

Coefficients of variation (CV) for some structural traits in some vertebrates and bees range from 1% to ~10% (47, 126, 204, 253). The CVs for some behavioral characters are similar to those for structure. These are Mayr's (137) "closed programs" (e.g. 0.07–11% for certain aspects of displays; 17, 204). For other behavior the CVs have higher values (e.g. ~13–33% for the number of elements in each song phrase in a songbird; or web characters of an orb-web spider; 59, 204). Slater (204) concluded that, in general, this measure shows behavior to be more variable than morphology (see 47 for problems with this measure, notably that the CV and the mean are not independent).

A useful way of classifying behavior according to its capacity for individual accommodation ("adaptability") follows Schmalhausen's (190) categories for morphogenesis:

1. *Autonomous ethogenesis*: There is essentially no influence of conditioning or experience on the development of the behavior pattern. If orb-weaver spiderlings, for example, are prevented from spinning juvenile webs, they

nonetheless spin normal webs as adults (see 74). Adult *Pieris* butterflies do not differ in flying ability, despite receiving more or less flight experience during their first five days of life (169).

2. *Autoregulatory-dependent ethogenesis*: Ontogeny is regulated by some information from the external environment. Imprinting is one example (11, 73). Although it is now recognized that many social factors (13, 14, 131, 235, 236) influence the timing and other aspects of the imprinting process, it is generally agreed that once an individual is “ready,” the presence of an appropriate external stimulus triggers the learning process, which then proceeds autonomously.

3. *Dependent ethogenesis*: Behavioral traits are partially determined in *direct* response to environmental stimuli. Imitative learning and teaching are its most highly developed forms, and they supply various instances of cultural transmission of information (24, 28, 256). Rapid horizontal transmission of information has great evolutionary significance, a point discussed below.

During the ontogeny of behavior, any deviations in developmental processes that alter the phenotype are potentially significant in providing, at the population level, a new context for the origin of evolutionary novelty, a point discussed by Mayr (135).

ACTIVE ROLES OF THE BEHAVING ANIMAL IN EVOLUTION

Various authors have suggested that the tempo of evolution is partly determined by the behavioral complexity of the group, or that behavior acts as a “pacemaker” of evolution (89, 136, 170). Darwin (49: p. 313) mentioned that forms on land “seem to change at a quicker rate than those of the sea,” and that animals “considered high in the scale of nature . . . change more quickly than those that are low.” Schmalhausen (190) gave examples suggesting that relatively passive sessile or floating animals are generally eliminated from the gene pool by *nonselective* destruction, resulting in higher fecundity (similar to fecundity in many plants). Haldane (92) illustrated *nonselective* destruction by comparing mortality in juvenile oysters and zebras, noting it is likely that a larger fraction of deaths is selective in zebras than in oysters: i.e. “if all baby zebras could be replaced by animals of the fittest genotype available, the juvenile deaths would be reduced by a larger fraction than if the same were done in oysters” (p. 189). Schmalhausen (190) argued that as individual activity increases, elimination increasingly involves *directional* selection (*r*-selection → *K*-selection; 163). One example he gave concerns mollusks. Major groups of Mollusca were well-differentiated at the beginning of the Paleozoic, and some are conservative with extant genera (e.g. *Neopilina*, Monoplacophora) known as fossils from the Cambrian. These forms appear to

have relatively simple behavior. Other mollusks (e.g. gastropods and cephalopods) are behaviorally more active and apparently have undergone higher rates of evolution (for conservatism in displays, 161). Stanley (209) reviewed other examples from bivalve mollusks and mammals that support Schmalhausen's views. These apparent rates of evolutionary change may be confounded by other factors, such as estimates of morphological complexity (197).

Examples from a variety of animals are given below to illustrate how preexisting structures become specialized or altered in phylogeny as a result of behavioral changes. In general terms the behavior of animals influences evolutionary change in one or more of the following ways (after 15).

Learning and Novelty

Many examples show the importance of prior experience for behavioral development (e.g. 16, 194, 195). Studies on mice, rats, fish, and insects show that winning or losing a social contest affects the ability to win subsequent encounters, mediated by alterations in hormonal titers and their influence on submissive or aggressive behavior (e.g. 36, 124, 189).

The phenotypic modifications of individuals can act synergistically with other behavior, generating variability for selection, especially during periods of stress (167, 168). Learning facilitates the acquisition of novelty, as shown by examples of feeding behavior (below) or the acquisition of song (e.g. 7). In some species, social learning results in rapid horizontal and then vertical transmission of information (26, 71, 256). An ability to learn allows an animal to exploit *any* other sources of novelty. The novel behavior is physiologically rewarded if it alleviates the stressful circumstances. Additionally, if the stress is severe and populations are greatly reduced in numbers, then the genetic bottleneck during subsequent generations creates conditions favorable for the chance fixation of a new trait (e.g. 96).

These learned modifications are evolutionarily important only if there is genetic variability among individuals for the behavioral and physiological abilities to cope with stress. That the required variability exists in natural populations is likely, based on examples in humans (27, 113) or birds (90), of behavioral and physiological reactions to unfamiliar events and effects of learning on dominance relations in tree shrews (102), rodents (19, 114), and other animals (167, 168, 189).

Wilson and colleagues (122, 185, 252) presented data showing that rates of chromosomal and anatomical evolution and of speciation are apparently correlated among major vertebrate groups. They noted that these rates have been higher for some groups (e.g. cichlid fishes, placental mammals) than others. Wilson et al hypothesized that these accelerated rates of divergence are associated with the relatively complex social behavior and learning abili-

ties of these animals, especially a capacity for cultural transmission of novel behavior. They discussed how “behavioral drive” and “social selection” can produce morphological change in populations, resulting from individual innovation and learned social transmission (also 77, 78).

To test their hypothesis, they examined the correlation between brain size (assuming it correlates with neural complexity) and anatomical divergence for 239 species of birds from 26 orders. Although they used two controversial measures (see 15, 172), they showed a positive relationship between complexity and divergence. In another study Sage et al (185) compared morphological divergence among cichlid fishes in Lake Victoria, and between these cichlids and North American centrachids (sunfish). They suggested that rates of morphological evolution in cichlids may be enhanced due to social transmission of information concerning feeding behavior. Social learning of feeding behavior has been experimentally studied in a serranid fish (5). Bluegills (*Lepomis*, Centrachidae) within a single lake display a complex foraging polymorphism involving behavior and structure, although its developmental basis is presently unknown (61):

Many of the “lower” animals (e.g. wasps) also have complex social behavior influenced by social factors not essentially different from those for vertebrates. Rats, for example, were only a little better than ants in learning a maze with the same topology (193). One important difference is that imitative learning has not yet been demonstrated for an invertebrate (195, 223, 256). Useful estimates for rates of morphological evolution are unavailable for social insects (see 107 for a biochemical example).

Active Choice in Social Situations

In many social situations animals make active choices which are not contingent on sophisticated learning abilities, yet nonetheless influence evolutionary change in populations. In other cases, learning is very important (e.g. 229a, 231).

COURTSHIP AND MATING BEHAVIOR Darwin (50) first described ways in which animals make *active* choices influencing character evolution in conspecifics. At first a contended point, there are now numerous examples of mate choice and other characters evolving under sexual and social competition (see 11, 220, 237), so only a few examples need to be given here.

Displays and ritualization Crane (46) studied the epigamic and threat displays of *Corythalia* (Salticidae) jumping spiders. In *C. xanthopa* males, the fourth legs (IV) are elevated only in a threat display and are prominently fringed with hairs; in the related *C. chalcea* these legs never leave the ground

in displays and are not fringed: these epigamic characters develop in the final instar. Using various models differing in morphological detail (dead spiders, cardboard), she showed that motion was more important than form in releasing display behavior in other males.

Crane (46) noted that if an appendage is exhibited in epigamic or territorial display it "usually shows some (morphological) differentiation which is to human eyes conspicuous." She further concluded that in salticids "display motions probably preceded most morphological secondary sexual characteristics, and that the latter often persist vestigially after they have ceased to function as part of the display stimulus configuration." Many examples in the ethological literature show that structure reinforces behavior (6, 21, 134, 136, 224). Structures used in courtship display do not necessarily become specialized (examples in 58) and usually do so only after they function primarily in a sexual context (224).

A second example involving spiders is of interest because it demonstrates genetic linkage ("stabilization") between behavioral and structural components of a display (also 198). *Schizocoza ocreata* and *S. rovneri* (Lycosidae) are wolf spiders that are virtually identical in external morphology, except for the first pair of legs (I) (212). Legs I of male and female *S. rovneri* lack any sort of conspicuous bristles. In this species the legs are never used in display; instead, a male contracts all eight legs simultaneously and "slams" its cephalothorax against the substrate (vibrations are an important component of the display). Male *S. ocreata*, in contrast, have tufts of bristles on their forelegs, and these legs are used in three different displays.

Males of both species attempt to court females of either species. Under natural conditions females mate only with males of their own species. Based on forced breeding experiments, female F_1 hybrids were morphologically indistinguishable from parental females. All hybrid males had tufts of bristles on the forelegs which were intermediate both in number and length of individual bristles, relative to the parental species. All F_1 males performed components of the displays of both *ocreata* and *rovneri*. In behavior and morphology, F_2 males fell into three groups: males with the *ocreata* phenotype, males with the *rovneri* phenotype, and intermediate males. Low (0–25%) rates of recombination in phenotypic proportions among the F_2 males and the backcross progeny suggest that the bristle character and the behavioral characters do not assort independently.

The countless examples of ritualized display are complex complementary series of changes concerning the motor patterns and structures of the actor ("sender") and the reactor ("receiver"). These have their origins in other behavior ("intention movements," etc), showing how changes in behavior select for genetic changes in structure. The categories of change fall into three major groups (from 21):

1. Changes in the stimulus required to release a behavior (due to changes in the threshold, context, etc).
2. Changes in coordination among the elements of a behavior (due to changes in frequency, intensity, or sequence).
3. Changes in the physiological relationship between the ritualized act and the inducer of the ancestral act, from which the motor pattern is derived ("stabilization" or changes in the causal factors controlling the expression of behavior).

Baerends (6) discussed how this process ("ritualization") has been unnecessarily restricted to describe social signals in a strict sense. He extended it to include flower-pollinator relationships. In turn, this can be extended to other types of behavioral evolution. A variety of noncommunicative behaviors, including host selection (below) and nest construction (68, 233), involve changes in sequences of behavioral acts, or changes in thresholds or stimuli that induce a given behavior.

Drosophila courtship Another example of behavior-induced divergence comes from fruit flies (Hawaiian *Drosophila* of the "adiastola" group) (38). Males of all species in the group eventually stand head-to-head with a female during courtship (207). As the level of sexual excitation increases, the male curls his abdomen over his head until it nearly touches the female's head. The abdomen is then actively vibrated. No obvious changes in external morphology are related to this, except in one species. In this species (*D. clavisetae*) the end of the male abdomen has long clavate hairs which are "swept" over the female's head. The species is found only on East Maui and is highly derived within the group, as judged by chromosomal relationships. Comparable *intraspecific* examples are known (e.g. 39).

Genitalic characters Eberhard (58) reviewed data showing that numerous patterns in the evolution of genitalia were largely inexplicable by a "lock and key" hypothesis. Available data better accord with a sexual selection hypothesis, under which the genitalia function behaviorally to provide tactile stimuli. As with characters used in displays, when genitalic characters are used in movements, they sometimes become modified with hairs and spines (also 179). The selective environment created by the female results in countless structural changes in male genitalia.

MARINE SYMBIOSES A species of damselfish (*Amphiprion*, Pomacentridae) involved in a symbiosis evolved at least 47 behavioral and physiological traits not seen in other pomacentrids not in symbiotic relationships (75; for other examples of symbiont-induced divergence, see 219). In symbiotic rela-

tionships each participant forms a part of the others' environment, showing how behavior creates an "environment" that influences subsequent evolution.

THE ORIGINS OF PARASITIC BEHAVIOR IN BEES "Social parasitism" is a broad class of behavior for which there is evidence to address criticisms raised by Simpson (see above), and for which the direction of evolutionary change (polarity) is obvious.

Numerous animals provide some sort of "parental care" for their offspring. Bees, for example, usually gather pollen and nectar, which they then store in a nest as food for their offspring. A derived state is easily recognized: Individuals invade nests of con- or hetero-specifics to exploit the parental behavior of other individuals (hosts), by causing the hosts to rear the parasites' offspring.

Of the 20,000 or so species of bees (an underestimate), approximately 15% are parasites of other bees (22). These species are often parasites of their close relatives and are more prevalent at high latitudes (see 230). They represent at least 26 independent evolutions of parasitism (W. T. Wcislo, unpublished).

Closely related facultative and obligate parasites show how behavioral changes in an ancestral population (e.g. invasion of another nest) *create* conditions that select for genetic changes in morphology, physiology, and behavior (below). Similarly, repeated group-living, like any other major "environmental" change, results in new situations in which natural selection influences evolution (e.g. 239).

Behavior Among free-living forms, *facultative* parasitic behavior is frequently observed without accompanying external morphological changes (Table I in 230). Facultative parasitic behavior can be induced by various environmental conditions, such as nest destruction, defeat in social competition, or asynchronous emergence in a seasonal area (e.g. 225a for bees, 117a for wasps). In other words, individuals of otherwise free-living species sometimes behave as parasites under certain environmental conditions. No studies presently available test for genetic differences between facultative free-living or parasitic individuals; in some species given individuals perform both behaviors (e.g. 231a, 239).

In *obligate* species this parasitic behavior is fixed, and all females invade nests of other species to deposit eggs. These females often have specialized (derived) behavior for entering nests, killing or dominating hosts, or laying eggs in peculiar locations (230).

Morphology The external morphology of *facultative* parasites is not differentiated from that of free-living conspecifics. *Obligate* parasites, in contrast, show varying degrees of divergence in internal and external adult

morphology, with respect to the ancestral condition. These obligate parasites tend to converge on a "suite of parasitic characters," which in bees includes loss of pollen-collecting structures, scythe-like mandibles, and a quadrate head with more massive mandibular muscles for killing hosts, a reinforced exoskeleton, and changes in ovarian physiology (see 147, 230). Structural features of a parasitic morphology can be induced in free-living individuals, to varying degrees, by perturbing the developmental system [e.g. topical applications of juvenile hormone (37, 116, 117), or by the presence of various pathogens (186)] (see 241 for ants).

Larvae of *free-living* bees usually have few specialized structures. Among parasitic species, if the adult parasite kills the host larva (e.g. Halictidae), then the parasite larvae show no divergent structural characters related to parasitic behavior (147). In contrast, if the adult parasite does not kill the host larva (e.g. some Megachilidae), then parasite larvae have specialized mandibles for killing the host larva or other parasite larvae. These mandibles develop in an early larval stadium and are lost at the next molt, usually rendering the larva indistinguishable from host larvae, which have the ancestral condition.

FEEDING BEHAVIOR AND STRUCTURES The behavior of animals in relation to food is extremely diverse, yet even a brief review of its components shows some general patterns. Brues (33) gave numerous examples of aberrant feeding behavior in insects (e.g. carnivorous caterpillars; or an east African moth larva [*Tinea*] that burrows into antelope horns where it feeds). He suggested four generalizations:

1. The change in feeding behavior from the "typical" pattern "frequently appears to be quite sudden and complete."
2. Evolutionary shifts in feeding behavior are rare, but occur more frequently when larvae are dependent on adults than when they are independent (i.e. "parental manipulation;" see 2).
3. Once established, shifts in feeding behavior are stabilized.
4. Shifts in feeding behavior are not "necessarily preceded or accompanied by essential anatomical changes in the mouthparts or other organs which are more or less intimately connected with feeding."

Reviews of vertebrate feeding behavior, and more recent studies of invertebrates, support these general conclusions, although there is disagreement over No. 4. These recent studies show that a greater emphasis should be placed on the importance of learning. Hinde (100) reviewed early studies of the ontogeny of feeding behavior in vertebrates (also 160). An excellent example of behavior-induced divergence involves the "upside-down" method

of feeding in flamingos, and the subsequent structural modifications of the bill (110).

Hunting wasps Female spider wasps (Pompilidae) hunt spiders as food for their offspring (except parasitic species). Some species are specialists, and others are catholic in their choice of spiders. Ferton (70) described the prey capture behavior of a wasp (*Pompilus [Entomobora]*) hunting trap-door spiders (Ctenizidae). The clypeus (lower face) is modified into "an elongate hook" which is slipped under the trap-door. The wasp flips her head, flinging open the door; she then enters and stings and paralyzes the spider. In another species, the wasp sometimes flips open the trap-door but often chews a hole through it (111). A species of *Aporus (Planiceps)* has the clypeus only slightly modified. A female enters a spider's nest by standing on the trap-door, grasping "the edge with her stout forelegs, standing nearly on her head, and then turning over . . . as though about to somersault," she dives into the entrance (246: p. 135 ff.). Williams did not mention if the clypeus is used to open the trap-door. It appears that whenever spider wasps specialize on trap-door spiders, a "spade-like" clypeus often later evolves. There are many independent evolutions of this structure in Pompilidae (M. C. Day, British Museum, *in litt*), although the biology of these species is poorly known. Other wasps (Sphecidae) nest in the ground, and have modifications on their forelegs for digging, which are lacking in nonfossorial forms (e.g. 176a).

Female sand wasps (Bembicinae) hunt other insects, and there are many examples of apparently species-specific ("innate") behavior involving prey carriage, prey choice and nesting behavior. Evans proposed models (68: Figure 215) to explain patterns of evolution in these wasps that are essentially similar to the hypothesis of Baldwin et al; they require behavioral flexibility in an ancestral taxon (e.g. 214).

Bees Bees (Apoidea) are a monophyletic group that arose from a sphecid-like wasp ancestor (130). Female sphecid wasps are predatory (some secondarily parasitic) and hunt other arthropods. A female stings the prey in a specific way and takes it to her nest as food for her offspring. Sometime in the middle lower Cretaceous, "sphecid" wasps were flourishing (130), and angiosperm plants evolved (~130 MyBP). In this altered environment a shift in "feeding preferences" occurred (plant food rather than insect food), and bees subsequently diversified (148). The diverse familial representation of fossil bees in Baltic amber (Eocene) indicates a relatively rapid diversification (radiation) for the group. Recently, this view was strengthened by the discovery of a fossil social bee (*Trigona prisca*) from late Cretaceous New Jersey amber (~80 MyBP) (152).

The most striking findings concerning the feeding behavior of bees are the

diverse morphological changes enabling a bee to extract pollen and other resources from flowers in which the resources are inaccessible. Secondly, many bees *learn* to remove resources which they otherwise would be unable to exploit. Comprehensive reviews are available for bees (34, 121, 146, 154, 222). Distantly related masarid wasps with the derived behavior of pollen-feeding also have derived structures for extracting pollen (162). These diverse morphological changes provide excellent examples of what Rensch (179) termed “undirected evolution” in morphology as a consequence of behavior-induced divergence (see 191 and 192 for examples of the reverse: structure-induced behavioral divergence). Evolution is “undirected” in that it is often difficult to predict exactly which structures will be altered in any given example (convergent evolution). Several examples follow.

Trigona is a large genus of small tropical social stingless bees. Nearly all usually collect pollen from anthers like normal bees. Sometimes individuals are “pollen gleaners” in that they will collect pollen from the surface of corollas where it falls after other pollinators have visited the flowers (154, 243). Bees in the subgenus *Scaura* are specialized for pollen harvesting as gleaners. They visit flowers with inflorescences having broad surfaces, or leaves below flowers. *T. (S.) longula* was observed at *Cassia* flowers (154); females visited the anthers only rarely, but when they did they collected pollen as would other *Trigona*. To collect pollen from leaf or corolla surfaces a female *Scaura* splays out her middle and hind legs so the inner surfaces of the basitarsi (“foot”) touch the flower; the unusually broad hind basitarsi are bent forward, even though the other segments of the hind legs (femora and tibiae) are directed backward. In this peculiar position the female “shuffles” over the substrate so that her hind legs and the distal part of her abdomen sweep the flower and collect pollen.

Bees can be placed in two informal groups. There are “short-tongued” bees, as well as “long-tongued” bees (+ Ctenoplectridae) which have elongate glossae and galeae (151). Other things being equal, a bee with a long “tongue” is obviously able to exploit flowers with long corollas. It can also exploit those with shorter corollas by standing up and extending the front legs while feeding (154). A short-tongued bee, in contrast, could exploit only those flowers with corollas as long or shorter than the length of their “tongue,” or those into which it can crawl. In bees, there is often a positive correlation between the length of the proboscis and the depth of the flower (94, 98, 217).

In the environments of “short-tongued” bees nutritionally acceptable flowers often have diverse corolla lengths (121). Species in various “short-tongued” lineages have evolved elongate mouthparts (i.e. “there are long-tongued short-tongued bees”). A variety of structures are changed in different species. For example, *Calothamnus* has a deep corolla and is principally bird-

pollinated. It is also visited by the "short-tongued" bee, *Euryglossa tubulifera* (Colletidae), which has enormously elongate maxillary palpi (~80% as long as head + body); the palps function to form a "drinking straw" to extract nectar (from 104, which also gives examples from other Colletidae, and a pergid sawfly).

Lastly, other bees in the families Melittidae, Ctenoplectridae, and Anthophoridae collect oil from plants. These bees use a variety of derived structures to extract and carry the material (34). Especially striking are *Rediviva* (Melittidae) bees which collect oil from the long spurs on *Diascia* (Scrophulariaceae) flowers in southern Africa. All segments of the front legs are elongate, with the more distal segments bearing dense "oil-mopping" hairs (226). Other oil bees gather oil with special combs on the first and second pair of legs, or on the abdomen; all these structural alterations are lacking in related non-oil-collecting bees.

The examples of apoid food-gathering structures and behavior reviewed above represent "adaptations", or genetic alterations of the peripheral organs and structures of the *Bauplan* of the group (in response to specific environmental situations). Any naturalist could list many examples for any taxa. The important conclusion is that changes in behavior likely precede the changes in structure (e.g. there are no long-legged *Rediviva* bees that do *not* collect oil from floral spurs). The general biological significance is that such anagenic changes potentially, but rarely, have macroevolutionary significance (see 135, 238).

Learning and food preferences Flowers provide a sensory-rich environment for bees, and provide visual, olfactory, gustatory, and tactile information (76, 143, 146). Based on both genetic studies and individual bioassays, differences in some specific learning abilities exist both within and among species. Bees are able to learn colors and are better at learning some colors than others. They learn shapes and may even form eidetic images, as do vertebrates (86); they also learn odors, textures, places, and compass direction (76). Bees are able to integrate this information in ways probably not fundamentally different from vertebrates (compare 142 with 208). They can be conditioned, or will habituate, to positive or negative stimuli in different contexts (1, 76, 231).

Various studies of honeybees (*Apis*) reported on artificial selection for good and poor learners for simple associations, with heritability estimates from 0.28–0.44 (29, 159). Genetic variation in learning abilities is significant because learning plays an important role in the development of food preferences, and therefore in foraging behavior. As a group, a colony of social bees uses pollen from a wide variety of plant species (146). Individual bees, at least in Apidae, however, tend to restrict their pollen-collecting to a single

species (floral constancy), either per foraging trip or over a longer period (98, 123, 146, 222).

Many *solitary* bees are restricted (“oligolectic”) in the pollen they collect. During ontogeny, the only experience with the preferred pollen source comes while feeding as a larva, or with what pollen remains in the larval feces after metamorphosis. Inexperienced adult bees of an oligolectic *Colletes* (Colletidae) showed a preference for the plant species on whose pollen they were reared, based on odors of whole flowers, whole pollen, or pollenkitt (external lipids); there were no preferences for internal lipids (53).

Rau (177) discussed examples of bees feeding on unusual pollen sources or obtaining resources in novel ways. He was especially interested in the apparently learned habit of nectar robbing, citing his own and others’ observations of bees and various birds. Bees pierce the flower with their mouthparts (proboscides) and suck out nectar without pollinating the plant. In some cases the environment is somewhat novel since many of the plant species that the bees rob are introduced species (9, 177).

Rau postulated that innovation was especially likely in times of stress (also 167, 168, 221). Under stresses due to the lack of the usual pollen source (e.g. from drought), a provisioning bee might die, become quiescent, or switch to new plants or resources in an opportunistic way. Many bees in the genus *Andrena* (*Diandrena*), for example, are oligolectic, usually collecting pollen from only one or a few species. Thorp (221) reviewed the pollen preferences of these bees and stated that “most of the alternative sources of pollen . . . were utilized only during periods of stress because of the absence or rarity of their preferred pollen source” (221, p. 29; also 153). These cases are of interest since learned habits might stabilize due to learning, if mating occurs at the flowers, a case known for some oligolectic bees (1a). Assortative mating at flowers may be enhanced by the reduced population size, assuming many bees die. Assortative mating which leads to reproductive isolation is necessary if a conditioned response is to become “instinctive,” a possibility discussed by Haldane (92, 93).

The role of learning for the establishment of novel feeding behavior is well-known in birds (e.g. great tits opening milk bottles, 101; also 118). Learning can function to make subsequent behavior either more or less “stereotyped.” Young chaffinches, for example, initially peck at spots within a wide size range when *not* hungry (when hungry they beg from parents); eventually, after being rewarded by obtaining food, they learn to peck only at “food-sized” objects (100). Similarly, young Darwin’s finches (various species) will feed in a variety of ways (presumably learned by imitating individuals of other species); later, these other behaviors are dropped as the species-typical behavior becomes stabilized, presumably from more efficient

handling and greater rewards (88). Various studies have reported a correlation between beak size and preferred seed size in birds (84, 88, 206).

The feeding behavior of birds may be influenced by positive or adverse conditioning, habituation, or social learning (e.g. 90, 115, 132, 223). Again, the important question involves how the range of food which a bird can *learn* to exploit is influenced by preexisting structures and motor patterns (e.g. 117b). Hinde (100) discussed an example from fringilline and cardueline finches: the chaffinch never uses its foot to hold objects, while goldfinches do so regularly and so can use it to manipulate food objects. He concluded that “small differences in diet between closely related forms” may be due to learned differences resulting from interactions between behavior and structure during development. Thorpe (223) reviewed other examples of birds learning to feed this way and noted that some species are better learners than others. An estimated 0.3% of passerine birds have abnormal bills as a result of developmental anomalies or injuries (173). In a sample of 48 abnormal birds in captivity, 40 learned to cope with the deformity and fed in novel ways. Few of the deformed individuals would be likely to survive under natural conditions.

An example relating learned feeding behavior and ecological opportunity occurs in the finches (*Pinaroloxias inornata*) on Cocos Island, Costa Rica (234). This is the only finch on the island and other potential competitors are rare. The range of feeding behavior within the species spans those of several mainland families. Individual birds, however, learn to specialize on one mode of feeding (paralleling social bees, in which the colony has generalized feeding habits, while individuals specialize).

“Invasion” of a Novel Environment

For animals the “invasion” of a novel environment is often by behavioral means (e.g. 136), and this shift entrains a series of changes significant for understanding evolution. A shift into a novel environment was experimentally studied by rearing fruit flies (*Drosophila*) in total darkness, starting in 1954 (~800 generations as of 1986) (60, 157, 158). Numerous genetic changes occurred in behavior (phototaxis, daily emergence rhythms, olfaction) and structure (fine structure of compound eyes, length of head bristles).

Other invasions of novel environments may be due to chance, and still others result from what Elton (64) referred to as “the selection of the environment by the animal,” or habitat selection. Another likely source of invasions of novel environments is *the selection of the environment by the parent*. Under certain circumstances, presumably stressful, parents manipulate their offspring (see 2) by placing them in a novel environment. One example involves a switch to a novel food source. The “manipulation” need not be

active but can result from other factors such as inconstancies of chemoreceptor sensitivities (196). Parentally induced shifts are also important because individuals of the same species can differ morphometrically in significant ways (e.g. length of ovipositor) when reared on different hosts (144). Morphology in turn potentially influences oviposition behavior (also 187).

HOST FIDELITY A general life cycle of many "parasitic" insects is that the parent female lays eggs on or in a host (a plant, fruit, another insect, etc). The egg hatches and the larva feeds on the host. Many studies have focused on the questions: To what extent are larvae conditioned to their food source as they feed? And do resultant adults display a preference for the same host when laying eggs?

Prior experience is known to be important in the establishment of feeding preferences ("host selection") in various insects, mainly due to adult learning; preimaginal (larval) conditioning occurs much less frequently (108, 166, 176, 223, 229). Some parasitoids (especially those unable to resorb developing eggs) will oviposit in alternative, otherwise rejected, hosts if they are stressed by being deprived access to the preferred host. This switching behavior has been induced experimentally in fruit flies (*Dacus*, Tephritidae) (72). In these flies some evidence suggests that odors from the host plant surface function as a feeding attractant for females and a sexual attractant for males, thus setting conditions for assortative mating (55; see above for oligolectic bees).

HABITAT FIDELITY Since work by Waddington and coworkers (see 227), various studies of "habitat" preference in *Drosophila* have shown: (a) Different species choose different habitats; and (b) both genetic and experimental factors influence habitat preferences, and the relative importance appears to vary among species (180, 181, 215, 216).

Habitat selection in birds and other vertebrates is well studied (44, 100, 160, 223, 232). Again, these reviews support the general conclusions reached from studies of insects. These findings on host and habitat selection can be summarized by stating that evolved sensory systems and locomotory abilities enable many animals to place themselves or their offspring in an environment where they can survive and reproduce. As a consequence, such individual behavior has great potential to influence population-level processes and evolution (models: 40, 85, 97, 103).

GROUP EFFECTS ABOVE THE LEVEL OF THE INDIVIDUAL

Many examples given above may belabor the point that animals modify their physical and social environments. If such modifications persist (e.g. repeated

group-living), then other behavior and morphology better suited to this novel environment will be selectively favored (239). Human beings and social insects provide excellent examples of animals with an amazing ability to alter their social and physical environment (18, 99, 240, 248, 249). An example illustrating behavioral control of the developmental environment comes from studies of caste determination in social insects. Additionally, it stresses again the point that the *degree* of control varies among species. In most species of Hymenoptera, each female has the potential to develop into either a reproductive “queen” or a sterile “worker.” Her fate depends upon the environmental conditions during growth and is mediated physiologically by hormonal titers (146).

Most colonies of stingless bees (Meliponinae) contain a single queen, and in most species workers build “queen cells” without prior experience. In these queen cells a special environment is created so that a female genome develops into a “queen” and not a “worker” morph. In stingless bees of the genus *Melipona* (e.g. *M. quadrifasciata*) caste determination is related to genetic differences among individuals, and queens are not reared in special environments (116, 146). Certain genotypes, however, can develop into either caste depending on environment. Since *Melipona* are highly derived bees within Apoidea (e.g. 244), this trait (partially genetic caste determination) is probably derived. Emerson (65) proposed this as an example of Waddington’s genetic assimilation.

Social relationships in bees other than Apinae are vastly more labile than previously believed (compare 146 with 149). Within species there is geographic variation in social organization with respect to latitude (150), altitude (188), or other factors relating to seasonality (62, 245). Within populations there are complex condition-sensitive alternatives available to females (i.e. facultative parasitism, 230; worker vs queen behavior, 146; or facultative diapause, 255; see 239). An individual’s reproductive success is determined by prevailing social conditions (e.g. see 109), which are themselves determined by feedback interactions among demographic, genetic, and environmental factors. Altmann & Altmann (3) made essentially the same point based on long-term studies of baboons at Amboseli. The feedback relationships between behavior and demographic factors, and social organization and life-history traits, imply that social structure determines which reproductive opportunities will be available to individuals (see 141 for population genetic consequences).

BELOW THE LEVEL OF THE INDIVIDUAL

Dover (54) proposed “molecular drive” as a mechanism for concerted genomic changes in multigene families, and he suggested the phenomenon was

important in producing evolutionary change. He hypothesized that concerted changes might generate morphological novelty and disrupt the historical relationships between organisms and their environment. Behavioral flexibility may allow accommodations for survival until genomic evolution stabilizes the changes from molecular drive (also 112). Similarly, molecular drive may generate behavioral variability per se, which then creates selective conditions for morphological evolution. In these models of molecular drive an important *transition* occurs between hierarchical levels.

Buss (35) suggested that transitions between hierarchical levels are evolutionarily significant because synergisms between levels generate variability, potentially enabling the organism to interact more efficiently with its environment (also 26, 59a). Variation in the organization of the higher unit (e.g. an organism) is partly determined by prior variation in the lower unit (e.g. genes), the traits “*expressed in the higher units now act as selective agents on the variation arising in the lower unit* (35: p.184)” (also 10, 59a). Discussing the evolution of individuality he noted how synergisms between selection at the cell lineage and individual levels might help explain the rapid evolution of the early Metazoa (e.g. Burgess shale fossils). Similarly, the ways by which complex behavior alters the mode or intensity of selection create potential synergisms between the individual and group (deme or population) level (see 247), possibly generating conditions for rapid evolution (122, 185, 252).

TESTING THE HYPOTHESES

The above examples help illustrate the indisputable conclusion that complex feedback relationships exist between changes in behavior and morphology, both in ontogeny and phylogeny. Evolutionary relationships between changes in behavior and structure can be tested by combining comparative behavioral studies with phylogenetic studies. A hypothetical example is given in Figure 1. Valid tests are possible only if the phylogenetic relationships are reconstructed *without* the behavioral and structural characters of interest (see 43, 242). Due to this condition, examples are difficult to find, partly because of divergent interests of ethologists and systematists (see 67, 134, 140, 145). For many groups whose behavior is well known, there are no rigorous phylogenies, and vice versa.

The potential utility of phylogenetic methods for testing these behavioral hypotheses was demonstrated by Brooks for studies of historical ecology (31, summarized in 32, also 52a). A phylogenetic analysis of 63 families of digenetic trematodes was used to ascertain whether “ecological diversification precedes or lags behind morphological diversification.” Brooks et al used six ecological categories and concluded that, historically, ecological (and therefore behavioral) diversification lags behind morphological diversification at

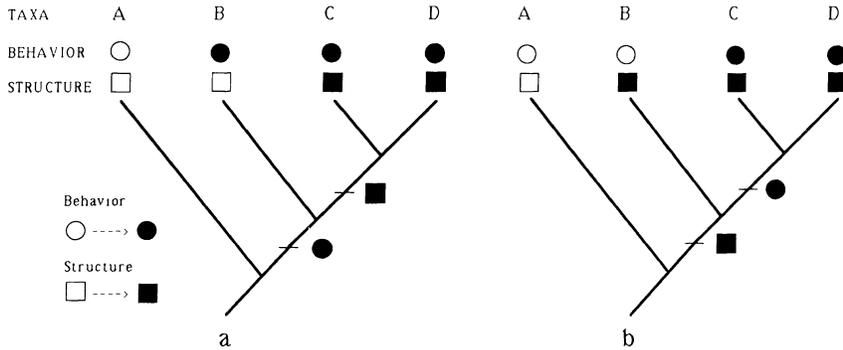


Figure 1 Alternative cladistic hypotheses relating evolutionary changes in behavior and structure. (a) A behavioral change precedes a structural change; (b) a structural change precedes a behavioral one. The topology of this tree is determined by characters other than the "structure" (SQUARE) and "behavior" (CIRCLE) to be tested.

the familial level. The methodology is useful, although a lower-level analysis would be more informative (4, 127) because monophyletic families and other higher taxa are "individuals" in a genealogical hierarchy, but not in an ecological hierarchy (63). Presently, however, studies of the behavioral ecology of individual trematodes are available only for a few economically important species (31, 213, 254). That lower-level analyses are necessary was demonstrated recently by West-Eberhard (238, 239a) who provided much evidence showing that novel characters can arise and diverge as stable "alternatives" or morphs *within* species. Many examples are associated with feeding behavior and other ecological shifts, usually associated with strong social competition (also 79, 155).

CONCLUSIONS

Behavioral adaptability is important in evolution because the activity of individuals has the potential to diminish or exacerbate the influence of external environmental heterogeneity. In either case, the selective environment in which the organism lives is modified.

Historically, the importance of behavior as an inducer of evolutionary change is not a new idea, but rather one that has yet to be fully woven into the fabric of evolutionary theory. An emphasis on the ontogeny of behavior suggests that development is important in evolution not only as an impediment to, or constraint on, evolutionary changes (as is frequently argued), but it is also important as an *facilitator* of change. Behavior-induced divergence is especially important in social (including sexual) behavior, feeding behavior,

and habitat and host selection. In most animals there is great potential for individual behavioral innovation resulting from alterations in developmental pathways during ontogeny. Furthermore, in many animals the innovation may spread by social transmission or other forms of learning. These innovations influence the nature of selection and other evolutionary processes. Recognizing the importance of behavior points to more realistic ways of thinking about the origins of divergence and the role of phenotypes in evolution.

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APPENDIX

The following excerpts are from Morgan (156):

“8. Let us suppose, however, that a group of organisms belonging to a plastic species is placed under new conditions of environment.

9. Those whose innate somatic plasticity is equal to the occasion survive. They are modified. Those whose innate plasticity is not equal to the occasion are eliminated.

10. Such modification takes place generation after generation, but, as such, is not inherited. There is no transmission of the effects of modification to the germinal substance.

11. But variations in the same direction as the somatic modification are now no longer repressed and are allowed full scope.

12. Any congenital variations antagonistic in direction to these modifications will tend to thwart them and to render the organism in which they occur liable to elimination.

13. Any congenital variations similar in direction to these modifications will tend to support them and to favour the individuals in which they occur.

14. Thus will arise a congenital predisposition to the modifications in questions.

15. The longer this process continues, the more marked will be the predisposition and the greater the tendency of the congenital variations to conform in all respects to the persistent plastic modifications; while

16. The plasticity continuing the operation, the modifications become yet further adaptive.

17. Thus plastic modification leads and germinal variation follows; the one paves the way for the other.

18. Natural selection will tend to foster variability in given advantageous lines when once initiated, for (a) the constant elimination of variations leads to the survival of the relatively invariable; but (b) the perpetuation of variations in any given direction leads to the survival of the variable in that direction”

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