

Developmental–Behavioral Initiation of Evolutionary Change

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The traditional approach to evolutionary psychology relies entirely on natural selection as the cause of the evolution of adaptations. Exclusive reliance on natural selection overlooks the fact that changes in development are a necessary prerequisite for evolutionary change. These developmental changes provide the material for natural selection to work on. In the neo-Darwinian scenario, the mechanisms of evolution are mutation or genetic recombination, selection, migration, and eventual reproductive isolation. In the spirit of evolutionary pluralism, the author describes a different 3-stage scenario in which migration (the invasion of new niches or habitats) may occur without mutation or genetic recombination and selection first initiating a change in genes or gene frequencies.

Adaptation and natural selection are central concepts in the emerging science of evolutionary psychology. Natural selection is the only known causal process capable of producing complex functional organic . . . adaptations. (Buss, Haselton, Shackelford, Bleski, & Wakefield, 1998, p. 533)

In contrast to the above, as first pointed out by Mivart (1871), adaptations arise before they are selected for and are therefore not a consequence of natural selection. Adaptations are a consequence of individual development; changes in individual development produce new behavioral variations and different adaptations. Thus, it is changes in individual development that produce evolution through natural selection. As noted by Endler (1986, p. 51), “natural selection cannot explain the origin of new variants and adaptations, only their spread.”

This article is about the role that behavior plays in instigating evolution; more specifically, the fundamental importance of changes in behavior brought about by changes in prenatal- and postnatal-rearing environments. Behavior is the leading edge of evolution, as has been intermittently recognized since the time of Lamarck (Leonovičová & Novák, 1987). Conventional thinking in evolutionary biology would hold that genetic mutations are the leading edge of evolution and that mutations change development and behavior. In the spirit of evolutionary pluralism, I am proposing a different pathway in which behavioral change leads the way to genetic change. These different pathways are not mutually exclusive.

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Selective Breeding for Behavioral Differences and Their Maintenance Across Generations by Stability in the Rearing Environment

Because genes are a part of the developmental system, of which behavior is also a necessary component, it is possible to selectively breed for any behavioral trait once that trait has surfaced. The evidence for that conclusion is presented in Table 1.

As seen in Table 1, it is possible to selectively breed animals for all kinds of existing behavioral differences: learning (maze dull, maze bright), spontaneous activity (high, low), audiogenic seizures (susceptible, nonsusceptible), alcohol preference (high, no preference), aggressiveness (high, low), mating speed (fast, slow), and so on. The differences in many of these strains (or lines) of animals developed rather quickly in the course of four or five generations of selectively breeding like to like. The trick is not in bringing about these line (strain) differences (selective breeding does that) but in maintaining the differences across generations. To maintain the differences, one needs not only to selectively breed the animals in each generation but also to make certain the prenatal- and postnatal-rearing conditions remain the same. If the genes alone were bringing about the behavioral changes, then the rearing environment would be irrelevant. However, because the genes do not make behavior, it is the genes-in-the-recurring-developmental-system that make for the stability of the behavioral changes across generations. The only reason it is possible to perpetuate virtually any trait by selective breeding in the laboratory is that great pains are taken to ensure that environmental (prenatal and postnatal rearing) conditions remain as constant as possible over the course of the generations of selective breeding. (It is important to note that not only adaptive traits can be selectively bred; pathological or disadvantageous traits are also responsive to selective breeding.)

The importance of controlling the rearing environment across generations was shown in a study by Hood and Cairns (1989), in which male mice were selectively bred for high or low aggression in dyadic tests in which two male mice are introduced to each other for the first time. During the course of selectively breeding for high and low aggression, the animals were reared in social isolation from the time of weaning until the dyadic test some three to four weeks after weaning. The investigators wanted to find out how

Table 1
Outcomes of Selective Breeding for Behavioral Differences

Species	Behavior	Source
Rats	Maze learning	Heron, 1935; Tolman, 1924
Mice	Speed in traversing runway	Dawson, 1932
Rats	Spontaneous activity (wheel running)	Rundquist, 1933
Rats	"Emotionality" in open field	Broadhurst, 1965; Hall, 1938
Mice	Sound-induced (audiogenic) seizure	Frings & Frings, 1953
Fruit flies	Orientation toward or away from light source (positive and negative phototaxis)	Hirsch & Boudreau, 1958
Rats	Saccharin preference	Nachman, 1959
Chickens	Aggressiveness	Guhl, Craig, & Mueller, 1960
Fruit flies	Components of courtship movements	Ewing, 1961
Fruit flies	Upward or downward orientation with respect to gravity (negative and positive geotaxis)	Hirsch & Erlenmeyer-Kimmling, 1961
Fruit flies	Mating speed	Manning, 1961
Mice	Alcohol preference	Rodgers & McClearn, 1962
Fruit flies	General activity	Manning, 1963
Honeybees	Nest cleaning, stinging	Rothenbuhler, 1967

important the social isolation period was in maintaining the line difference in aggression, so they reared half of the males from each line in social groups from weaning until testing. As shown in Figure 1, there is a large difference in attack frequency between the high- and low-line mice when they are reared, as usual, in social isolation (left side of Figure 1), but this difference disappears entirely when the high-line mice are reared in social groups. The findings hold for both testing in the home cage as well as in a neutral cage under both rearing conditions.

Therefore, once a new behavior has arisen or manifested itself, it can be perpetuated by selective breeding and a recurring developmental medium. However, how does the new behavior arise in the first place?

The Developmental Induction of Novel Behavioral Phenotypes

Since the 1950s, developmental animal psychologists have demonstrated repeatedly that varying the early experiences of young animals alters their behavioral phenotype, even into adulthood if the rearing environment supports such persistence. The earliest of these studies concerned the "handling" of rodents in the preweaning period (0 to 3 or 4 weeks of postnatal age). The so-called handling procedure involved separating the pups from their mothers for a few minutes each day during the preweaning stage of development. Although there were species and strain differences, by and large, handled animals benefited from this intrusion, showing heightened exploration, increased resistance to stress, and improved learning ability in adulthood (Denenberg, 1969; Levine, 1956). It turned out that the most important mediator of the handling effect was the pronounced "extra" mothering (e.g., grooming) that the handled pup received on return to the nest. The handled pups emitted ultrasonic vocalizations when they were returned to the nest, and females became particularly solicitous when hearing these vocalizations (Noirot, 1964). In studies that did not involve human intervention, Ressler (1963, 1966) found strain differences among mice in the amount of maternal handling of

offspring, and his findings on later effects in adulthood coordinated well with the findings from the human intervention studies: maternally handled offspring (BALB strain) outperformed offspring in the less maternally handled strain (C57BL) in operant barpressing and visual exploration. Ressler's findings of a trans-generational effect are of special significance in the present context: The grandchildren of both strains did well when their grandparents were of the BALB strain (foster BALB grandparents in the case of the C57BL mice).

In brief, to summarize the very extensive handling literature, this experience results in relatively stress-resistant animals that would be capable of exploration (instead of freezing) and of

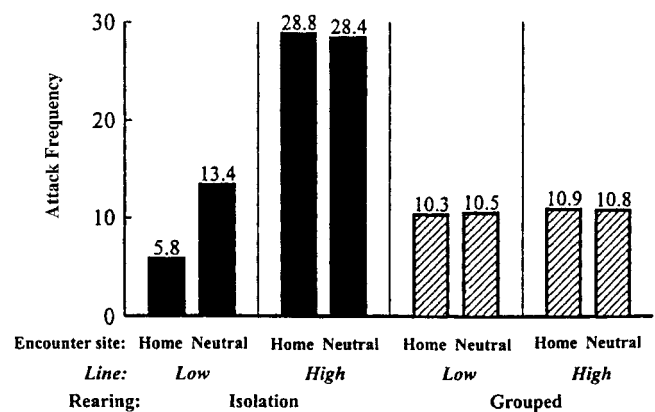


Figure 1. Failure to maintain selectively bred line difference in aggression when rearing environment changed from social isolation (usual rearing environment) to social grouping. Data are from Hood and Cairns (1989). Adapted from "The Significance of Biology for Human Development: A Developmental Psychobiological Systems View," by G. Gottlieb, D. Wahlsten, and R. Lickliter. In *Handbook of Child Psychology: Theoretical Models of Human Development* (p. 249, Figure 5.9), by R. M. Lerner (Ed.), 1998, New York: Wiley. Copyright 1998 by Wiley. Adapted with permission.

adaptive learning when faced with a completely strange and unfamiliar environment in adulthood. The research showed that the axis between the hypothalamus and the adrenal and pituitary glands was enhanced by the handling experience and that this anatomical–physiological change was correlated with the handled animal being able to tolerate greater stress in adulthood. Denenberg (1969) and colleagues showed that the handling experience had to occur early in development if it was to be effective. Animals subjected to the same experience at older ages did not benefit from the experience, as indicated by later tests of resistance to stress and of exploratory behavior.

Another experimental intervention that creates novel behavioral phenotypes through changes in development is the so-called “free” or environmental enrichment paradigm, in which, once again beginning in the 1950s, developmental animal psychologists began exposing rodents to what were called “enriched early rearing environments” and examining the effect of the experiential manipulations on changes in brain size and brain biochemistry and on problem-solving ability in adulthood (for a review, see Renner & Rosenzweig, 1987). In 1952, Hymovitch showed definitively how enriched early experiences are crucial to later problem solving in adulthood. In this pioneering study, Hymovitch reared young rats under four conditions and later tested them in the difficult Hebb–Williams maze. (He might not have gotten any effects of early experience if he had tested their learning ability in much simpler learning tasks, such as a Y maze or a T maze.) The animals were housed individually in (a) a stovepipe cage that permitted little motor or visual experience, (b) an enclosed running or activity wheel that provided a lot of motor experience but little variation in visual experience, or (c) a mesh cage that restricted motor activity but allowed considerable variation in visual experience as it was moved daily to different locations in the laboratory. The fourth group was made up of 20 animals that were reared socially in an enriched environment that was very large (6 ft × 4 ft [1.83 m × 1.22 m]) compared with the other conditions and was fitted with a number of features (blind alleys, inclined runways, small enclosed areas, apertures, etc.) that offered the rats a wide variety of opportunities for motor and visual exploration and learning in a complex physical and social environment (labeled *free environment* in Tables 2 and 3). The animals lived in these four environments from about 27 days of age to 100 days of age, at which time testing in the Hebb–Williams maze was completed. The results of testing are shown in Table 2.

As seen in Table 2, rearing in the stovepipe and the enclosed running wheel led to the same level of poor performance, whereas rearing in the mesh cage and the free environment led to the same

Table 2
Errors in Hebb–Williams Maze of Rats Reared Under Four Different Conditions

Condition	No. of errors
Stovepipe	223
Running wheel	235
Mesh cage	140
Free environment	137

Note. The stovepipe and running wheel groups made significantly more errors than the other two groups. Data are from Hymovitch (1952).

Table 3
Errors in Hebb–Williams Maze of Rats With Different Early and Late Environmental Experiences

Early/late experience	No. of errors
Free environment/stovepipe	161
Stovepipe/free environment	248
Free environment/free environment	152
Normal cage/normal cage	221

Note. The stovepipe/free environment and normal cage/normal cage groups made significantly more errors than the other two groups. Data are from Hymovitch (1952).

level of good performance over 21 days of testing in the Hebb–Williams maze. All the groups also showed the same level of improvement over the 3 weeks of testing, therefore the animals reared in the mesh cages and free environment began functioning at a superior level early in the testing.

To determine whether it was the early experience in each environment that made for the differences among the groups, Hymovitch (1952) repeated the experiment with four groups of animals that differed in when they had the free (enriched) environment or stovepipe experience: One group had the free-environment experience from 30–75 days of age and then were placed in the stovepipe for 45 days, a second group had the stovepipe experience from 30–75 days and then had the free-environment experience for 45 days, a third group remained in the free environment throughout the experiment, and a fourth group remained in their normal laboratory cages throughout the experiment. This last group was the most thoroughly or consistently deprived from the standpoint of motor and visual experience.

As seen in Table 3, the animals that experienced the free environment early and the stovepipe later in life performed just as well as the animals that remained in the free environment throughout the experiment. The crucial finding was that the animals that experienced the stovepipe environment early and the free environment later in life performed as poorly as the animals that remained in their normal cages throughout the experiment (the most deprived group). It is important to note that these differences in problem-solving ability were not evident when Hymovitch (1952) challenged the rats with a simpler alley maze, more like the ones that were widely used in most animal learning laboratories at the time. It was only when they were challenged by the much more difficult Hebb–Williams series of problems that the differences in problem-solving ability were evident.

It was not long before these early experience studies were extended to other animal species, including nonhuman primates, where social isolation and otherwise highly restricted, deprived rearing conditions were used. Indeed, even in primates with relatively large brains, the normal or usual variety of experiences early in life was critical for the appearance of normal exploratory and learning abilities later in life. Deprived infants showed severe deficiencies in their later behavior (Harlow, Dodsworth, & Harlow, 1965). Just having a large brain is insufficient for the development and manifestation of the superior problem-solving skills characteristic of primates (Mason, 1968; Sackett, 1968).

Thus, behavioral plasticity that is essential to the genesis of new behavioral phenotypes is dependent on variations in early experi-

ence (as well as possessing a large brain, as reviewed earlier in Gottlieb, 1992, chap. 14; Gottlieb, 1997, chap. 9). The conditions that favor the appearance of a behavioral neophenotype are severe or species-atypical alterations in environmental contingencies early in life (Kuo, 1976). These changed contingencies can arise in two ways in animals living in nature: (a) some sort of physical or geographical change happens to (is forced on) the animal (a disruption of habitat, climactic change, etc.) and, probably more frequently, (b) the migration of the animal into a somewhat different habitat on the basis of normal exploratory behavior. The animals that are more likely to withstand (a) and commit (b) are ones that have had not only traditional but also nontraditional variations in early experience. To put it the other way around, exposure to conservative or narrow social and physical environmental contingencies early in life will make animals less likely to withstand (a) and unlikely to perpetrate (b). These predictions on evolutionary readiness, as it were, follow from the results of the early experience studies reviewed previously.

The Repetition in Adulthood of Familiarity-Inducing Early Experience

As first recognized by psychoanalysts and called a *repetition compulsion*, there is a developmental dynamic that causes humans (and other animals) to prefer the familiar and thus to strive to reinstate early life situations or repeat versions of their early life experiences in adulthood, a psychological process akin to imprinting. Consequently, it could be that animals that have had considerable variation in their early social and physical experiences tend to seek out such variation in adulthood—just what is needed to heighten exploratory behavior and encourage novelty seeking! Although actual developmental experiments have not yet been done to show that animals (including humans) that have had considerable variation in their early experience tend to seek out novel experiences as adults, there are two studies of adult mammals and birds that show that novelty is a psychological dimension of experience that can be abstracted, such that animals so trained consistently prefer to interact with novel rather than familiar objects or situations when given a choice (Honey, 1990; Macphail & Reilly, 1989). From the present theoretical perspective, it would be most valuable to validate the developmental induction of novelty-seeking behavior in later life through the experience of considerable variation early in life. (I have benefited from discussions of this idea with Professor Gerald Turkewitz of Hunter College.)

In anticipation of the material reviewed in the next section, I wish to elaborate on the familiarity-inducing experiential mechanism described above. It has long been recognized that there is a form of learning that takes place through mere exposure to physical and social objects; the exposure leads to subsequent attachment, preference, or acceptance of these objects (i.e., animals and humans not exposed to these objects do not show attachment, preference, or acceptance of them). This familiarity mechanism, termed *exposure learning* (Sluckin, 1965), is pervasive; it is found in many invertebrate species as well as vertebrate species (Szentesi & Jermy, 1989), and it is often referred to as *imprinting*, although, technically speaking, imprinting involves a sensitive period early in life and is usually defined as inducing an enduring preference, not merely acceptance (nonavoidance) of an object (or an experi-

ence). Although particularly striking in young animals (Sluckin, 1965), exposure learning operates throughout life in some species such as our own (Hebb, 1946; Rheingold, 1985; Zajonc, 1971). Psychologically speaking, exposure learning (the acquisition of familiarity) is above the level of the lowest forms of learning—habituation and sensitization—in that it requires a higher degree of perceptual differentiation and longer term memory. It would almost always be adaptive to form attachments, preferences, and acceptance of familiar physical and social objects.

An Example of the Developmental–Behavioral Basis of Evolution: Incipient Speciation in Two Variants of the Apple Maggot Fly

A shift into a new niche or adaptive zone is, almost without exception, initiated by a change in behavior. The other adaptations to the new niche, particularly the structural ones, are acquired secondarily . . . This is not the place to discuss how the behavior changes themselves originate, a problem still poorly understood. (Mayr, 1963, pp. 604–605)

In the preceding sections, I have sketched a theory of how such behavioral changes could originate. An empirical example of incipient speciation mediated by a transgenerational, developmental change in behavior is provided by the apple maggot fly (*Rhagoletis pomonella*). The original native (United States) host for the female apple maggot fly's egg laying was the hawthorn, a spring-flowering tree or shrub. Domestic apple trees were introduced into the United States in the 17th century. Haws and apple trees occur in the same locale. The first known infestation of apple trees by apple maggot flies was in 1860. There are now two variants of *R. pomonella*, one that mates and lays its eggs on apples and the other that mates and lays its eggs on haws.

As shown in Table 4, the life cycles of the two variants are now desynchronized because of the fact that apples mature earlier than haws. Incipient speciation began, and likely has been maintained, by a transgenerational behavior: something akin to, but not as straightforward as, an imprinting-like olfactory preference (i.e., a familiarity-inducing early rearing experience) for courting, mating, and ovipositing on the host in which the fly developed (reviews in Bush & Smith, 1998; Prokopy & Bush, 1993).

We can only speculate on the cause of the original shift from hawthorns to apples as the host species for egg laying. Perhaps the hawthorn hosts became overburdened with infestations or, for other reasons, died out in a part of their range, causing a shift to apples on the part of a small segment of the ancestral hawthorn population that did not have such a well-developed olfactory sensitivity that would have led to an olfactory aversion to apples. This latter supposition is supported behaviorally as well as physiologically. In behavioral tests, the apple variant accepts both apples and haws as hosts, whereas in the haw variant, only a small percentage accept apples and most show a strong preference for haws (Luna & Prokopy, 1995; Prokopy, Diehl, & Cooley, 1988). To substantiate the olfactory basis of host selection, early studies showed that the flies are strongly attracted to specific odors emanating from the host fruits (Prokopy, Moericke, & Bush, 1973).

Volatile esters isolated from whole fruit extracts have been shown by electroantennogram (EAG) assays and behavioral observations to be important in eliciting the response to fruits . . . It is therefore clear

Table 4
An Example of the Developmental–Behavioral Basis of Evolution: Incipient Speciation in Two Variants of Apple Maggot (Fruit) Fly (Rhagoletis pomonella)

Time	Apple host	Hawthorn host
Year 1	Eggs laid ↓ Fruit matures earlier than haw	Eggs laid ↓ Fruit matures later than apple
Year 2	Hatch late ↓ Summer 5 to 12 days ↓ Offspring court and mate on or near host, and female lays eggs on same host	Hatch early ↓ Fall 5 to 12 days ↓ Offspring court and mate on or near host, and female lays egg on same host
Year 3	↓ Cycle repeats	↓ Cycle repeats

Note. Based on Bush and Smith (1998) and Prokopy and Bush (1993).

that *R. pomonella* flies use chemical cues to find host fruits and that olfactory information transmitted from antennae play a significant role in this process. (Frey, Feder, Palma, & Bush, 1998, p. 176)

The original shift from haws to apples, presumably by a small number of less sensitive individuals, fits nicely with the current finding that the apple variant is less sensitive to odor differences than is the haw variant (Frey et al., 1998).

Furthermore, . . . within the volatile region found to be attractive to *R. pomonella* by Fein, Reissig, and Roelofs (1982), the chemical profile[s] of apples and hawthorns are fairly similar, which could have facilitated the original shift of the fly to apple (Carlé, Averill, Rule, Reissig, & Roelofs, 1987). Nevertheless, certain chemical differences do exist between the two fruits (Carlé et al., 1987), affording the possibility that the fly races are exploiting these differences when deciding between fruits. (Frey et al., 1998, p. 176)

Given the repetition–compulsion or exposure-learning mechanism described earlier, in which adults reinstated familiar sensory stimulative, perceptual, and/or cognitive features of their early experience—a familiarity-reinstatement or imprinting-like process—in the first generation, some portion of the male and female offspring of the original apple flies, if not all, accepted apples for courtship, mating, and egg-laying and thus, through this developmental–behavioral means, perpetuated the initiation of the potential evolution of a new species of *R. pomonella*. Admittedly, we can not know in this case the factors that contributed to the original selection of the apple host in Generation 0; otherwise, the present information conforms to the developmental–behavioral evolutionary hypothesis advocated in this article.

My reason for saying that the imprinting-like olfactory preference is not straightforward is that the behavioral experiments done so far indicate that rearing on the apple host does not actually create a preference for the apple host, but, rather, the exposure learning renders the apple host more acceptable (less aversive) to

the apple variants, so they will accept both apples and haws as hosts when the opportunity presents itself in laboratory and field experiments that manipulate the environment in such a way as to bring about a choice test (Luna & Prokopy, 1995; Prokopy et al., 1988). Therefore, it is the familiarity-inducing (exposure-learning) rearing experience, perhaps coupled with the reduced olfactory sensitivity of the apple variant, that sustains the apple variant's choice of the apple as host. A similar hypothesis has been put forth by Frey et al. (1998, pp. 182–183), although they believe the rearing experience induces a preference, whereas I think the existing data support an acceptance of, rather than a preference for, the apple host.

In a seminaturalistic experiment, Luna and Prokopy (1995) created four separate patches of trees with either apples or hawthorn fruits and released hawthorn-reared or apple-reared flies into one of the patches. This was an acceptance test rather than a preference test because only one fruit was available in each patch, as would be the case in nature. The apple-reared variants did not differ from the hawthorn-reared variants in the number of eggs laid in the hawthorn patches. However, in the apple patches, the hawthorn-reared variants laid only 20% as many eggs as the apple-reared variants. This result is significant in that it shows not only that the apple-reared variants have a greater acceptance of apples but also that a small percentage of the hawthorn-reared flies accept an apple host, as must have been the case when apples were noticeably infested for the first time in the mid 1800s.

Most of the behavioral experiments with the apple maggot fly have been done with female flies. In a behavioral experiment with male flies, Prokopy et al. (1988) found that, in an acceptance test, young apple-reared males remained significantly longer on apples than young hawthorn-reared males, thus supporting the field observations that apple-reared males stay around apple trees and are therefore likely to court and mate with apple-reared females (Prokopy & Bush, 1993).

Further evidence that the rearing experience of the apple variants makes them more accepting of the apple host—but does not actually instill a preference for apple over hawthorn—comes from experiments in which apple-reared and hawthorn-reared females were given acceptance tests (one host present) and true-preference tests (both hosts present) and their egg-laying behavior was tallied (Prokopy et al., 1988, Table 1). In both kinds of tests, a greater percentage of the flies displayed egg-laying behavior (i.e., boring their ovipositor into the fruit) in the hawthorn host, irrespective of their rearing experience. Clearly, then, the apple-reared flies do not have a preference for the apple host over the hawthorn host, as would be the case if they were truly imprinted by their rearing experience. Rather, as indicated in the single-host acceptance tests, the apple-reared flies show a greater percentage of egg-laying behavior on the apple host than do the hawthorn-reared flies. Thus, the familiarity-inducing rearing experience (exposure learning) makes the apple-reared flies more accepting of the apple host, although they still maintain a preference for the hawthorn host. Their actual preference for the hawthorn host is shown in the tests with both hosts present: They show as high a percentage of egg-laying behavior on the hawthorn host as do the hawthorn-reared flies, and the same lower percentage of egg-laying behavior on the apple host as the hawthorn-reared flies, regardless of whether they visited only one or both hosts. The fact that the rearing experience of the apple flies does not truly imprint an

olfactory preference but rather extends the range of acceptable odors was also found in experiments with fruit flies (*Drosophila* species; Manning, 1967). In that study, once again, rather than the early experience of a novel odor creating a preference for that odor, the early experience merely reduced the level of later behavioral avoidance of the odor (i.e., made it more acceptable).¹

Therefore, for terminological correctness, the acceptance of a wider range of odors of potential hosts induced by the apple-rearing experience should not be considered an instance of olfactory imprinting but rather the induction of olfactory familiarity through exposure learning that increases the likelihood of acceptance of the apple host in adulthood. Given the ecological circumstances, the increased likelihood of acceptance of the apple host, even in the face of a preference for hawthorn, would work just fine to perpetuate the transgenerational courting, mating, and laying of eggs in apple orchards. As described by Prokopy and Bush (1993, p. 6), apple maggot flies hatch out at the base of the tree where their mothers had laid their eggs the previous summer. While becoming sexually mature in the next two weeks, they wander around the vicinity of the apple orchard to forage for food. When they become sexually mature, even though they have wandered tens or hundreds of yards, they are still in the vicinity of the apple orchard, if not still in the orchard. The scent of the apples attracts them, and the early rearing experience having rendered the apple scent acceptable, the cycle renews itself because of the high probability that the early maturing apple maggot fly will encounter the odor of apples rather than hawthorns (see Table 4 for the desynchronized life cycles of the apple and hawthorn variants). The two variants are now genetically somewhat distinct and do not interbreed freely in nature although they are morphologically the same and remain interfertile.²

In contrast to the transgenerational behavioral scenario presented here, as mentioned in the introduction, conventional evolutionary-biological thinking would hold that "most likely some mutations in genes coding for larval-pupal development and adult emergence" brought about the original divergence and maintains the difference in the two populations (Ronald Prokopy, personal communication, August 2000). Although it is not something anyone can know with certainty in this case, present evidence suggests that a genetic mutation was not necessary. This is not a behavior versus genes argument because the transgenerational behavioral initiation requires genetic compatibility, otherwise it would not work. The question is whether the original initiation (switching to the apple host) required a genetic mutation or not. The developmental timing change in the life histories of the two *R. pomonella* forms (described in Table 4) has resulted in correlated genetic changes in the two populations (allele frequency differences: Feder, Roethele, Wlazlo, & Berlocher, 1997). That finding is consonant with the evolutionary model presented here (i.e., gene frequencies change some time after the behavioral switch). From the present point of view, another significant feature of the findings of Feder et al. is that when immature hawthorn flies (pupae) are subjected to the prewintering environment of the apple flies (pupae), those that survive have a genetic makeup that is similar to the apple flies. Most important, this result shows that there is still sufficient individual developmental-genetic variability in the hawthorn population, even at this late date, to support a sheerly transgenerational behavioral initiation of the switch from hawthorns to apples without the necessity of a genetic mutation.³

In summary, a behavioral change involving the apple maggot fly's choice of oviposition site gets it into a situation where it must be able to withstand certain prewintering low temperatures for given periods of time (that differ between the apple and hawthorn forms; see Table 4). This situation sets up the natural selection scenario that brings about changes in gene frequencies correlated with the prewintering temperature regimen, as demonstrated in the Feder et al. (1997) experiments. Therefore, it is the change in egg-laying behavior that leads the way to genetic change, the genetic change being a consequence of the change in behavior, as advocated in this theory.

Conclusion

In conclusion, I have presented evidence to show that the first stage in the pathway to evolution is a change in ontogenetic development that results in a novel behavioral shift (a new behavioral phenotype) that recurs across generations, encouraging new environmental relationships. In my hypothesized second stage in the evolutionary pathway, the new environmental relationships can bring out latent possibilities for anatomical or physiological change. Somatic mutations or changes in genetic regulation may also occur in this stage, but a change in structural genes need not occur at this stage. A change in genes may occur in the third stage of the evolutionary pathway, resulting from long-term geographic or behavioral isolation (separate breeding populations). It is important to observe that, in this theory, evolution has already oc-

¹ Another reason for emphasizing that the early experience of the apple maggot fly merely influences the olfactory acceptability of hosts for oviposition rather than imprinting a preference is that the adult fly continues to be open to experience. Namely, the egg-laying experience of adult apple maggot flies influences their preferences for familiar perceptual features (e.g., visual) of the host on which they have already laid some eggs (for a review, see Prokopy & Papaj, 2000, pp. 239–240). (This species lays one egg at a time.) The mature fly's openness to perceptual experience beyond olfaction would thus reinforce (extend) the olfactory influence stemming from the larval feeding experience by building other perceptual features on it in adulthood. Thus, in this species, the exposure-learning, familiarity-inducing perceptual mechanism continues to operate in adulthood, embracing other senses besides olfaction. The early olfactory influence orients the mature fly to prospective egg-laying sites, and the visual experience consolidates the egg-laying preference.

² In order not to digress from the main point of this essay, I have not discussed the controversial subject of allopatric (geographical) versus sympatric (nongeographical) speciation. *R. pomonella* is an incipient example of sympatric speciation (Bush & Smith, 1998). An insightful review of the allopatric-sympatric controversy, and especially the different roles ascribed to behavior in the two views, is provided by Kremencov and Georgievskij (1987).

³ The apple maggot fly story is presented in the literature as an argument in support of the controversial notion of sympatric speciation. The hawthorn and apple forms are not yet recognized as two species. The field observations and laboratory experiments with the apple maggot fly are consistent with the developmental-behavioral theory of evolutionary change advocated in the text and are presented to add some further credence to that pathway. No one has challenged the field and laboratory findings as such. I leave it to others to argue the merits of the case for sympatric speciation (e.g., Bush & Smith, 1998). Although the present theory happens to be supported by a sympatric species, I do not regard it as necessarily restricted to sympatric speciation.

curred phenotypically at the behavioral, anatomical, and physiological levels before the third stage is reached.

Hence, new variations and adaptations arise before they are selected for and are therefore not a consequence of natural selection, as Buss et al. (1998) and other authors have claimed. New variations and adaptations are a consequence of changes in individual development mediated by transgenerationally persistent changes. In this view, natural selection is not the cause of the new adaptations but acts only as a filter through which the new adaptations must pass. Changes in behavior create the new variants on which natural selection works. As noted in the introduction, "natural selection cannot explain the origin of new variants and adaptations, only their spread" (Endler, 1986, p. 51). And, as Mayr (1963) remarked, novel behavioral shifts antedate the anatomical changes, which arise secondarily, in the evolution of new species. The contribution of the present theory is to offer a developmental scenario to bring about the novel changes in behavior and an explanation of how such changes can be maintained across generations without any initial change in genotype.

Finally, it has been suggested that I should comment on the relationship of the present theory to the culture-gene coevolutionary theories of Lumsden and Wilson (1981) and Boyd and Richerson (1985). Although there is some similarity among the theories (e.g., an explicit interest in individual development), Lumsden and Wilson do not advocate that developmentally induced changes in behavior antedate natural selection and genetic change, which is the major contention of the present theory. Rather, in common with traditional evolutionary-biological theory, Lumsden and Wilson rely on natural selection instilling the genetic changes that are then followed by changes in development (genetically determined epigenetic rules in the case of Lumsden and Wilson, 1981) and changes in behavior. Boyd and Richerson differ from Lumsden and Wilson in viewing culture and genes as independent inheritance systems (dual inheritance systems). The role of individual development in Boyd and Richerson's theory is primarily addressed to the perpetuation of cultural traditions through social learning and imitation (maintaining the status quo and maintaining differences between human populations). Boyd and Richerson regard the population-genetic theory of traditional evolutionary biology as entirely adequate for the genetic-selection inheritance system. With respect to changes in human behavior and culture, they say that "traditions are modified by accident, individual choices, and natural selection" (Boyd & Richerson, 1985, p. 291). In Boyd and Richerson's theory, the operation of natural selection on variants in the cultural-inheritance system is considered analogous to its operation in the genetic-inheritance system. I do not think that Boyd and Richerson would object to the notion that developmentally induced changes in behavior antedate natural selection and genetic change. I think that notion is compatible with their thinking; it is just not a major concern in their theory.

In an extension of Boyd and Richerson's (1985) dual-inheritance theory, in Durham's (1991) coevolutionary theory, it is clear that behavioral changes through cultural influences can alter gene frequencies in the sense of the population-genetic point of view shared with conventional evolutionary biology. In Durham's theory, the role of individual development in the process is not detailed (social learning is invoked in a general way), but clearly that role could be invoked in a substantial way. The present model I advocate aligns to some degree with the recent coevolutionary

theory of Laland, Odling-Smee, and Feldman (2000), which emphasizes that humans (and other animals) have the capacity to modify sources of natural selection in their environment (niche construction) by means of cultural (or protocultural) changes operating through learning and other experiential processes during individual development. The idea that the species' niche (construed broadly) is constructed anew in each generation is felicitous in that it brings development to the fore, and it squares nicely with the apple maggot fly story. My own theorizing departs from Laland and colleagues when they leave developmental considerations out of the picture with notions of "genetically guided niche construction" (p. 133) and "animals are genetically predisposed to respond" (p. 138), concepts that smack of the outmoded idea of a genetic program for behavioral outcomes. Thus, as pointed out by King (2000), the theoretical outlooks could be made more compatible if Laland and colleagues adopted a more fully coactional development system in describing the relationship between genes and behavior (Gottlieb, 1991).

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