Adaptive Behavior

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Adaptive Behavior 1993; 2; 5

DOI: 10.1177/105971239300200102

Parental Guidance Suggested: How Parental Imprinting Evolves Through Sexual Selection as an Adaptive Learning Mechanism

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The study of adaptive behavior, including learning, usually centers on the effects of natural selection for individual survival. But because reproduction is evolutionarily more important than survival, sexual selection through mate choice (Darwin, 1871) can also have profound consequences on the evolution of creatures' bodies and behaviors. This article shows, through simulation models, how one type of learning—parental imprinting—can evolve purely through sexual selection, to help in selecting appropriate mates and in tracking changes in the phenotypic makeup of the population across generations. At moderate mutation rates, when population tracking becomes an important but still soluble problem, imprinting proves more useful and evolves more quickly than at low or high mutation rates. We also show that parental imprinting can facilitate the formation of new species. In reviewing the biological literature on imprinting, we note that these results confirm some previous speculations by other researchers concerning the adaptive functions and evolutionary consequences of imprinting. Finally, we discuss how sexual selection through mate choice may have great scientific implications for our understanding of the interactions among evolution, learning, and behavior, and potentially important engineering applications for increasing the efficiency of evolutionary search and optimization methods.

Key Words: sexual selection; imprinting; mate choice; evolution; learning; speciation

1 Introduction

The concept of natural selection has a central place in the study of adaptive behavior. Much of the research done on adaptive behavior, both in empirical biology (e.g., Krebs & Davies, 1993) and in computer simulation (e.g., Meyer, Roitblat, & Wilson, 1993), focuses on the individual's ability to survive in a challenging environ-

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Adaptive Behavior Vol. 2, No. 1, 5–47

ment, by assessing how well it does in the important tasks of finding food, avoiding predators, negotiating obstacles, and so on. Adaptive behaviors such as these will be shaped through evolution by the natural selective forces acting on the individuals that emit them. However, as Darwin (1871) himself emphasized, reproduction can, in many instances, prove more important than individual survival because reproduction determines which genes will survive and replicate beyond the inevitable death of the bodies in which they are carried (see Dawkins, 1982). Because reproduction in sexually reproducing species is usually mediated by selective mate choice, various forms of sexual selection through mate choice (Darwin, 1871) can also have profound consequences on the evolution of creatures' bodies and behaviors. Compared to natural selective pressures, sexual selective pressures emerge from different sources (mate choice mechanisms rather than econiches), influence different kinds of traits (perceivable courtship displays rather than other aspects of phenotypes), and result in very different evolutionary dynamics (capricious runaway processes rather than convergent hill climbing); for these reasons, sexual selection cannot be subsumed under natural selection as a "special case" (see Miller, 1993a).

The ability to learn is a paradigm case of a behavioral capacity whose evolution is usually explained through natural selection (e.g., Bolles & Beecher, 1988; Davey, 1989; Marler & Terrace, 1984; Staddon, 1983). Learning in living systems is typically said to have the adaptive function of allowing adjustment to important changes in a creature's environment that happen faster than evolution can track. As such, learning can evolve through natural selection in species where it gives individuals an advantage in finding changing food supplies, avoiding new parasites, or navigating newly acquired territories. Indeed, in our own previous work, we have focused on the evolution by natural selection of learning mechanisms that have a direct effect on the survival of individual creatures (Miller & Todd, 1990; Todd & Miller, 1991a, 1991b).

Yet learning could also evolve *without* natural selection, spreading through a population solely under the pressure of sexual selection. Rather than tracking rapid changes in the environment, learning could evolve to help individuals track changes in the current composition of the *population*, thereby helping individuals to find suitable mates. In terms of sexual selection theory (see Cronin, 1991), learning could evolve as part of the preference mechanism that influences mate selection rather than as part of a courtship trait (such as a peacock's tail) that results from mate selection.[1]

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[1] It is also conceivable that learning could evolve as the sexually selected trait itself, by animals mating preferentially with others who showed certain learning abilities. In this case, a learning capacity per se would be elaborated as a courtship display, but there is no evidence that this has ever happened in any species. However, special learning mechanisms could certainly arise by helping individuals learn more effective courtship displays, as when male birds learn bird-song, or when rock musicians learn new guitar riffs to attract groupies.

In this article, we present evidence for just such a scenario. We show how the learning of mate preferences by parental imprinting can evolve in a population of simulated creatures that are subject solely to sexual selection, not natural selection. Some types of learning may thus arise by enhancing the chances of reproduction rather than survival.

Evolution certainly shapes the adaptive behaviors, such as learning, that creatures perform, but we are also interested in the way those behaviors can shape the course of evolution. Elsewhere (Todd & Miller, 1991c; Miller & Todd, 1993a) we have explored the ways in which simple behavioral mechanisms of mate choice can have profound macroevolutionary effects: Populations can split into new species, runaway processes can lead whole populations to evolve wild phenotypic elaborations, and individuals converged to stable peaks in the natural fitness landscape can be forced from their perches to careen downhill to lower survival, but higher reproductive, success. Such findings show how the usual direction of causation from evolution to behavior can be reversed, such that behavioral mechanisms influence the course of evolution. Here we combine both of these research programs—the evolution of learning capacities and the effect of learning capacities on evolution—by looking at the evolution of mate choice mechanisms that depend on learning. As we will see, sexual selection can favor the evolution of parental imprinting as an adaptive mate choice mechanism, and the new sexual-selection dynamics that arise in populations of imprinters can affect the large-scale course of evolution, facilitating the formation of new species. These complex interactions between evolutionary dynamics and learning mechanisms mean that adaptive processes cannot be arranged in a simple linear hierarchy where evolution affects development which affects learning which finally affects behavior (cf. Miller & Todd, 1990). Instead, evolved psychological mechanisms such as perception and learning can feed back into evolution in various surprising ways (on this point, also see Endler, 1992; Guilford & Dawkins, 1991; Miller, 1993a; Miller & Freyd, 1993; Plotkin, 1988; and Ryan, 1990).

In the remainder of this article, we first discuss the nature of parental imprinting and its adaptive functions in the service of choosing good mates to enhance reproductive success. We then present our modified genetic algorithm model for studying the evolution of this type of learning and show how and why imprinting does indeed spread through the population in our simulations. Next we discuss the macroevolutionary effects that such learned mate preferences can have on the further evolution of the population. Finally, we consider some of the further implications of this research, both for the scientific study of evolutionary processes and adaptive behavior and for the design of complex autonomous agents (e.g., robots) using simulated evolution. Our primary goals here are to show, through simulation models, how an adaptive behavioral capacity can evolve via sexual selection rather than natural selection and how such a behavioral capacity, once evolved, can affect the further course of evolution by influencing the dynamics of sexual selection.

2 Imprinting and Mate Preferences

2.1 Biological background

There are several types of learning that facilitate the selection of mates in many different species. They cover a wide range of processes and uses, including novelty-seeking mechanisms that bias an individual's preferences toward previously unencountered classes of potential mates (including the presidentially inspired Coolidge effect [see Dewsbury, 1981]), mechanisms for copying the observed mate choices of others (Pruett-Jones, 1992), and mechanisms that allow culturally influenced preferences in humans (see Fisher, 1992). We focus here on the phenomenon of *sexual* or *parental imprinting*, in which the sexual preferences exhibited by individuals later in life are learned through exposure to other individuals, usually a parent, at a very young age. Sexual imprinting is seen most frequently in certain birds and has been studied extensively among these species (Immelmann, 1972). It has also been suggested in some mammals (Immelman, 1972), and considered but generally discounted in fish, particularly cichlids (Siepen & Crapon de Caprona, 1986; Barlow, Francis, & Baumgartner, 1990). A vivid (though still controversial[2]) example is that of the lesser snow goose, which occurs in two color phases, blue and white. These geese seem to prefer mates that match the coloring of their parents rather than themselves (Cooch, 1961; Cooke & McNally, 1975). If an individual of one color, say blue, is raised by foster parents of the other color, i.e., white, its preference will usually follow that experience, and it will later seek white mates.

Similar cross-fostering experiments with other sexually imprinting species have succeeded in creating preferences of one species for another: Pigeons raised by doves, for example, will later prefer to court other doves rather than members of their own kind (Sluckin, 1973, pp. 54–55). Indeed, sexual imprinting is a technique used to help induce otherwise unmating species to create new hybrids. Researchers including Lorenz (1935/1970) have created still more pathological instances, getting birds to sexually imprint on their human experimenters (and in fact, according to Ridley [1987], one of the reasons Lorenz used greylag geese in many of his studies was that they could be *socially* imprinted on him without also *sexually* imprinting and thereby subjecting Lorenz to unwanted copulation attempts). Hawks are also subject to such imprinting; falconers take advantage of this by wearing special hats to collect the sperm of their amorous human-imprinted male charges for use in breeding programs (Moser, 1990). Thorpe (1956) even reports the case of "a gander's alleged

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[2] Barlow and colleagues (1990) argue that imprinting has not been proved in this case.

seven-year fixation to an oil-drum" (p. 365). Cases such as these obviously tell us more about the power of the out-of-context learning mechanism than about the function it serves under normal conditions.

2.2 Sexual versus filial imprinting

Sexual imprinting is similar in some regards to the more commonly discussed phenomenon of *filial imprinting*, in which the young of many species develop an attachment to their parents that is manifest primarily through following behavior (Hess, 1959, 1973). Both types of imprinting occur only during a sensitive period early in the individual's lifetime, and both are relatively permanent and difficult to alter. Because of these similarities, some researchers have rolled the two phenomena into one, which shifts from the associated behavior of following in early life to sexual responses later in adulthood (Sluckin, 1973, p. 127). However, the differences between these two types of imprinting are significant and probably indicate that they are separate adaptations.

First, the sensitive periods of filial and sexual imprinting may differ, with the latter usually coming later and lasting longer (Immelmann, 1972). Second, the relative permanence of learning is much more pronounced with sexual imprinting: Whereas filial imprinting and the behavior of following one's parent usually wane with maturation, sexual imprinting has been found to last, in zebra finches at least, beyond the natural lifetime of these birds in the wild (Immelmann, 1972, p. 156). Third, sexually imprinted preferences tend to generalize widely, often applying to all potential mates within one's species, while filial imprinting is usually directed toward specific individuals.[3] Finally, as Lorenz (1935/1970) pointed out, the effect of filial imprinting is seen immediately, whereas sexual imprinting does not usually exert its influence until well after the imprinting experience has occurred, most commonly after sexual maturity.[4] As a consequence of all these differences, we may provisionally consider sexual imprinting as a distinctive, domain-specific, adaptive learning mechanism.

2.3 Two dimensions for analyzing imprinted mate preferences

2.3.1 Specificity of mate preferences To put sexual imprinting learning in the proper context, we need to analyze mate preferences in general along two distinct dimensions: specificity and origin. The adaptiveness of having appropriately specific

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[3] Note, in this regard, that sexual imprinting is not the same as an Oedipus complex (Freud, 1913/1950), since it applies to a parent's traits rather than to the parent as an individual. In fact, there are probably powerful evolved pressures *against* sexually imprinting on one's parents as particular individuals, to discourage inbreeding (see Thornhill, 1991, and Bateson, 1978, 1983). Also, sexual imprinting is different from the sort of parent-offspring bonding studied by Bowlby (1969) and Harlow (1971).

[4] This and other factors also make it difficult to explain sexual imprinting as a standard form of conditioning to a reward, as some have tried to do for filial imprinting. Hess (1964, 1973) further argues against the claims that either type of imprinting can be subsumed under associative learning.

mate preferences is clear (see Darwin, 1871; Cronin, 1991). By choosing mates wisely, rather than randomly, an individual will have a better chance of genetic representation in the next and subsequent generations; a poor choice could result in few, if any, offspring.

At the most general end of the specificity spectrum, mate preferences could be set up such that one is sexually receptive to every opposite-sex member of one's entire species (as males of many species are). If the preferences are any more general than this they could lead the individual to waste energy and protoplasm on untenable conjugations. (Note, though, that because females are generally much choosier than males, males account for most interspecies copulation attempts—see Trivers, 1985, and Eberhard, 1992.) This degree of generality promotes mating with the maximum number of potential conspecifics, but it has the disadvantage of still allowing trysts with some potentially very undesirable partners, such as close kin or genetically defective individuals. Being pickier may often be wiser. For instance, preferences can be restricted to a particular morph (a body type or "race") within a species, usually one's own. These choosier preferences can yield positive assortative mating (like mating with like), which can in turn increase the viability of the individual's offspring by fostering ecological specialization and avoiding disruptive selection between different morphs (Dobzhansky, 1937). This may be the case in the lesser snow goose, where each color type could have correlated adaptations to different ecological subniches (Cooch, 1961). Morph preferences (mediated by different songs) have also been suggested as an explanation for polymorphism and niche specialization within some species of Darwin's finches and as a possible mechanism for their sympatric speciation (Grant & Grant, 1979), a topic to which we will return in section 6.

Mate preferences can be yet more specific, by forming the search image for one's ideal mate from the phenotypic traits of a few selected individuals. One's parents may provide a useful mate search-image as they were, after all, successful enough to have at least one offspring (i.e., oneself). The same could hold true of siblings and other commonly encountered family members, although their reproductive success is not as clear as that of one's parents. Having mate preferences based on closely related family members could help to maintain coadapted gene complexes via inbreeding; but there may be an optimal compromise between inbreeding and outbreeding, such that mate preferences that are biased slightly *away* from one's parents and sibs may be most adaptive (Bateson, 1978, 1983). (The urge to find mates similar to one's parents could possibly be influenced by gene-level selection effects on the parents themselves, who might promote their own genes by biasing their offspring to seek mates likely to be carrying those genes. The offspring, though, could well have opposing genetic interests of their own. The possibility of this sort of parent-offspring conflict in parental imprinting has not yet been investigated.)

2.3.2 Ontogenetic origin of mate preferences As we have seen, mate preferences can vary in specificity from the extremely general (mate with anyone of the right species) to the extremely focused (mate only with individuals resembling one's parents or kin). However, they can also vary along the dimension of ontogenetic origin, ranging from inheritance to experience. At one end, we have inherited "hard-wired" preferences, genetically encoded and not subject to modification by learning. This type of preference is very common, occurring throughout the animal kingdom. Indeed, almost all existing models of sexual selection assume genetically fixed preferences (e.g., O'Donald, 1980; Lande, 1981; Kirkpatrick, 1982; see Bradbury & Andersson, 1987, and Cronin, 1991). The need for inherited preferences is particularly clear in species that might otherwise be able to learn their preferences but whose behavior makes such learning impossible: For instance, cowbirds and cuckoos, who lay their eggs in the nests of other species using a strategy called *brood parasitism*, must show an innate mate preference for their own species as they are never exposed to conspecifics to learn about as they grow up (Cushing, 1941).

Inherited preferences are often fairly broadly focused, serving to pick out conspecifics from heterospecifics. By assessing potential mates on the basis of a few fairly clear sensory signals (simple key stimuli, as Lorenz [1935/1970, p. 243] proposed), inherited preferences can allow mating with a wide range of individuals. In contrast, preferences for specific traits that are displayed by a more restricted set of individuals, such as one's close relatives, would be difficult to pass on genetically. This is because in species with sexual recombination, the specific traits that distinguish parents in one particular genetic lineage from those in another will tend to vary substantially across generations. For the inheritance of a parental preference to work without any learning of the parent's appearance during the lifetime, there would have to be extremely tight genetic linkage between the perceptual traits characteristic of parents in a lineage and the sexual preferences for those traits. Although this sort of genetic linkage between trait and preference can, if it evolves incidentally, become strong enough to drive runaway sexual selection in a species (Fisher, 1930; O'Donald, 1980; Lande, 1981; Kirkpatrick, 1982), it could not be relied on to be specific enough to ensure mating with an individual that resembles one's parents.

At the other end of the origins dimension, mate preferences can be learned.[5] Learned preferences can be fairly broadly tuned, as in the cases mentioned earlier of

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[5] In this article, we focus on a type of mate preference mechanism that is clearly tuned through learning rather than set genetically. Nonetheless, most mate preferences in nature probably fall somewhere intermediate on the ontogenetic origin dimension, implemented by a complex inherited mate choice mechanism (including sensory, perceptual, memory, decision-making, and behavioral components) with a few of its decision-making criteria shaped by learning. And it must be remembered that all learning, including parental imprinting, presupposes the existence of a complex, evolved, fairly domain-specific mechanism that determines what to learn, under what conditions, according to what reinforcement criteria (Cosmides & Tooby, 1987; Miller & Todd, 1990).

sexual imprinting on an entire species or subspecies morph, but they can potentially be much more specific, tuned to the specific traits or identities of a few particular individuals, in a way that inherited preferences probably cannot. For example, to achieve an optimal degree of outbreeding, it may be useful to learn the identities and appearances of one's parents, siblings, and close kin. Alternatively, there may be substantial benefits to copying the specific mate choices of other more experienced individuals, thereby attuning one's preferences to the current patterns of mate choice and reproductive success manifest in the population (Pruett-Jones, 1992). Neither parental imprinting nor mate choice copying can be achieved without some mechanism capable of learning.

However, with learned mate preferences, as opposed to inherited ones, we must also specify *from where* the preferences are learned. In the case of preferences for the traits shown by particular individuals (e.g., parents, siblings, oneself, or sexual superstars), the model for learning is clearly the relevant individual, but for learned preferences that are more broadly tuned, to cover entire morphs, populations, or species, what should be the perceptual input to the learning mechanism? Sampling problems might arise. An individual could learn a broadly tuned preference by taking itself as a prototypical case; it would at least be guaranteed that it had chosen a learning model of the correct species. Difficulties would ensue, though, for sexually dimorphic species, which would end up imprinting on the wrong (same) sex if they used this learning method. Also, self-scrutiny is difficult for individuals lacking mirrors, though self-imprinting may sometimes be possible given long necks (or reflective pond surfaces?), for example, for domestic fowl (see Vidal, 1982) and some fish (see Barlow & Rogers, 1978). Alternatively, the individual could learn about the appearance of its species from others, but how can it guarantee that it is selecting a model of its own species in the first place? A simple answer is for the creature to learn its preferences only when it is most probably around conspecifics. In species with parental care, this condition will be most easily fulfilled soon after birth, when the individual is likely to be in the presence of its parents, who are definitely conspecifics. Parents, then, are particularly good role models even for learning mate preferences that are broadly tuned to the entire species: They are necessarily sexually mature adults of the proper species, they are available to learn from (in species with parental care), and they have actually demonstrated their ability to reproduce, indicating that they are at least not total losers.

3 Sexual Imprinting and Its Adaptive Functions

Sexually imprinting on one's parents could thus fulfill two different functions in tuning up one's mate preferences: learning about one's parents in particular or learning about the species more generally. In the former case, the adaptive function of sexual imprinting could be to achieve greater fitness by getting the right balance between inbreeding and outbreeding, as Bateson (1978, 1983) suggests. However, optimal outbreeding theory relies on detailed assumptions about the fitness effects of various genetic combinations (e.g., lethal homozygotes caused by inbreeding), which we chose not to model in this work; our interest here lies solely in the effects of sexual selection, which allows us to avoid the additional complexities that natural selection would bring. (We have, though, elsewhere considered the macroevolutionary effects of mechanisms that could produce optimal outbreeding, based on preferences for mates that are somewhat dissimilar from oneself [see Todd & Miller, 1991c].)

The second case, where parental imprinting allows learning of more broadly tuned mate preferences, points toward other possible adaptive functions. Immelmann (1975) suggests one reason such learned preferences may prove superior to inherited preferences: learning may allow a greater amount of information to be passed from the parents to their offspring than does genetic storage: "The amount of information that can be stored in the genome is rather small as compared with the possibility of information storage in the memory" (p. 245). In this case, the child is essentially using the appearance of its parents as part of its extended phenotype (Dawkins, 1982), relying on their presence to help program a portion of the perceptual motor mechanism that underlies selective mate choice. (Here, parental imprinting may be more akin to the type of learning that wires up the visual system of newborn kittens and other animals in response to early visual input; see Miller & Todd [1990] for a general discussion of such adaptive functions for learning.)

3.1 Information transmission

To support this claim about the relative information-transmission ability of genetics versus learning, Immelmann (1975) cites evidence that males and females imprint somewhat differently in many species. In ducks, pigeons, and finches, among others, the preferences of females are found to be much less influenced by their early parental experience than are the preferences of males. This may be due, Immelmann says, to the fact that the males of these species are typically much more conspicuous in their plumage, calls, displays, and so forth, so that females may easily recognize them by means of a few salient cues, which could be genetically transmitted. Females, on the other hand, tend to be much more cryptically colored and less behaviorally extravagant (Darwin, 1871; Wallace, 1889) so that males need "a more precise knowledge of the opposite sex that, obviously, can be obtained only through individual learning" (Immelmann, 1975, p. 245). McFarland (1987) concurs, saying, "For innate recognition to be reliable, conspicuous sign stimuli are probably necessary. . . Among [sexually dimorphic] species the females are generally less susceptible to imprinting, relying more on innate recognition of members of the opposite sex" (p. 305).

This line of reasoning, though, is problematic for a number of reasons. First, it is confounded by the observation that the young birds typically have more exposure to the female parent caring for them than to the male. The claims about relative amounts of information storage in the genome and memory are also difficult to assess; as Johnston (1982) warned, "arguments based on the information encoding capability of the genome tread on very insecure ground" (p. 77). Nor has empirical evidence been collected on this score. Lacking relevant data, it is difficult, at this stage, to see how to construct a simulation model that could test this hypothesis accurately; the costs of memory versus genome storage could be manipulated so that either one came out the adaptive winner. We thus cannot address the pertinence of this possible function until additional data are amassed. Furthermore, the argument seems to buy into a long-discredited notion (e.g., that of Mayr, 1942) that the primary function of female choice is to ensure mating with a male of the right species. On the contrary, all the available evidence, both from observations on the sexual ornaments of males (Darwin, 1871) and from direct experiments on the preferences of females (see Cronin, 1991), suggest that females in almost all species make much finer discriminations among potential mates than do males. Thus, the information about male appearance that they inherit cannot be automatically assumed to be any less detailed than the information males *learn* about female appearance.

3.2 Environment tracking

A second, more compelling adaptive function of sexual imprinting could be that it allows individual behavior to somehow track important environmental changes faster than is possible through evolution of the genotype. This is the most commonly postulated adaptive function of learning in general (e.g., see Bolles & Beecher, 1988; Davey, 1989; Marler & Terrace, 1984; Staddon, 1983). Thus, the location of good food patches, the quickest route to the home burrow, the color of poisonous berries, or the sounds that approaching predators make might all change more rapidly than evolution can track—perhaps even within an individual's lifetime—so the faster adaptive process of learning may prove beneficial. However, in the case of sexual imprinting, the environmental variable tracked by learning would be *the population itself*, specifically the current frequency distribution of viable phenotypes. That is, sexually imprinting on the phenotypes of one's parents allows mate preferences to follow ongoing population dynamics directly with only one generation of lag-time.

If one phenotype proves very successful in a particular generation—for example, the blue form of the snow goose—sexual imprinting will allow all the offspring of that phenotype to learn preferences for it. This allows them to avoid mating with lower-fitness individuals of different phenotypes, to prefer mating with higher-fitness individuals resembling their manifestly successful parents, and thereby to have offspring with higher-fitness genes. Genetically fixed mate preferences would evolve much more slowly in response to shifts in the population, and individuals with such fixed preferences would be less well calibrated in their mate choice and so would tend to have fewer offspring and ones of lower viability or attractiveness. Immelmann (1975) highlights these advantages of imprinting: "Any changes in the environment of a species, including the appearance of the species itself, are followed automatically by a corresponding change in the relevant object preferences, if the latter are acquired through personal experience. . . This is of special importance in rapidly evolving groups of animals as well as in unstable environments where a fair degree of opportunism will be favoured as compared with absolutely rigid preferences for particular conditions" (p. 245).

It is this "opportunistic" population-tracking function of sexual imprinting that we explore with the model presented here. This function is most closely linked to the naturally selected scenarios we have previously investigated (Todd & Miller, 1991a, 1991b) and is most amenable to the the realm of sexual selection that interests us in this work. In addition, if parental imprinting facilitates population tracking, this should have intriguing macroevolutionary implications; in the most extreme cases, it could result in the formation of new species, as we will see. We begin to look at this adaptive function of sexual imprinting by investigating the conditions under which this form of learning might evolve through sexual selection.

Simulating the Evolution of Sexual Imprinting

Our method for simulating the evolution of sexual imprinting is somewhat different from that used in our previous simulations of the evolution of learning (Miller & Todd, 1990; Todd & Miller, 1991a, 1991b). There we used the genetic algorithm to evolve simple neural networks that controlled the behavior of simulated organisms in simulated environments and that could learn about those environments to guide adaptive behavior. The model we develop here diverges from the previous studies in two major ways. First, to emphasize the role of sexual selection in the evolution of the populations we use in this study, we have completely eliminated nonsexual selection—that is, we have a completely flat fitness landscape, with each individual equally viable. The forces that drive evolution will come through the number of mating opportunities that each individual is able to obtain and exploit. This means the standard genetic algorithm has been modified, both eliminating differential viability between individuals and changing the way in which individuals are chosen for crossover and representation in the next generation. Second, we do not use neural networks to simulate the learning mechanisms of creatures in this scenario. Rather, sexual imprinting is modeled by simply making the child's ideal mate preference equivalent to the phenotype of one of its parents, as described later. Because this type of imprinting is so straightforward, the use of neural networks would unnecessarily complicate the simulation and cloud the theoretical issues.

4.1 Representation and expression of traits

Each individual in our simulations has a genotype made up of just six genes: two *trait* genes coding for phenotypic attributes, two *preference* genes coding for the preferred phenotypic attributes of potential mates, one *choosiness* gene coding for the amount of deviation tolerated from the specified phenotypic mate preferences (i.e., how far an individual will generalize its sexual receptivity from its ideal during its mate search), and one *learning* gene indicating whether the actual mate preference values are genetically determined or parentally imprinted. Using two phenotypic dimensions for the traits and preferences makes visualization easy: The phenotype of each individual can be represented as a single (x, y) point on a two-dimensional plot, the individual's mate preferences can be represented as a circular region (whose radius is specified by the choosiness gene) around another (x, y) point, and the phenotype frequency distribution of an entire population can be represented as a set of points in the same space. We interpret the two-dimensional phenotype space as a toroid of 1000×1000 arbitrary units (where the top edge connects to the bottom, and the left edge to the right). It is imperative to remember that positions in this abstract two-dimensional phenotype space are not spatial locations in physical space and that separation in this space cannot be interpreted geographically. Mate preferences permitting, it is as easy for two individuals far apart in phenotype space to mate as for two individuals close in this space.

By constructing the phenotype space as a toroid, all locations have equal prominence, eliminating center biasing and edge effects. Also, all of the genes are Gray-coded. For the genes corresponding to x and y positions in phenotype space, Gray-coding has the appealing property of making each edge of the space just one mutation away from the corresponding opposite (and toroidally connected) edge; for example with four bits, the bit-string 0000, which codes for 0.0, is one mutation away from the bit-string 1000, which codes for the phenotypically equivalent 1000.0. The Gray-code representation is thus smooth in our toroidal phenotype space (which would not be true of normal binary coding).

4.2 Representation and expression of preferences

After the first two genes specify the individual's location in phenotype space, the rest of the genotype determines the individual's *mate preference function*. First, the location of the individual's ideal mate must be assigned. If this mate preference is evolved (i.e., the learning gene is "off"), then the ideal mate location is simply that coded in the individual's preference genes: it uses whatever preferences it inherited. However, if this mate preference is to be learned (the learning gene is "on"), then parental imprinting occurs: the ideal mate location for this individual is assigned to be the actual phenotypic location of one of its parents. The two offspring created for every pair of parents each imprint on a different parent. This imprinting mechanism is evolutionarily unbiased in that the variance of imprinted preferences tends to match the variance of phenotypes in the population, so in the absence of sexually selective pressures, the population mean and variance for both traits would tend to remain stable over generations.

Once this ideal mate location in phenotype space is decided, either by inheritance or learning, the choosiness gene tells just how far away from this ideal the individual would be willing to settle in choosing a mate, as we will describe shortly. Note that there is no differential "storage cost" here between having the preference information inherited in the genotype or learned in the phenotype, so our simulation will be unable to illuminate whether imprinting evolves to save genotypic storage space, a possible adaptive function discussed in the previous section. Because the population can move about in phenotype space, though, we can investigate the population-tracking function.

The mate preference function maps the phenotypic distance between the individual's ideal mate location and some potential mate onto a probability that the individual would actually choose to indulge in this mating opportunity. The closer a potential mate is to the individual's ideal mate location, the better the chance that the individual will choose to mate. Thus we have implemented sexual imprinting so that offspring prefer an exact match to their parents but can also allow a significant amount of deviation from that ideal, via the evolved choosiness parameter. We use a mate preference function in which the probability of mating falls off linearly with increasing distance between (1) the phenotypic location of the ideal preferred mate (as genetically specified or imprinted) and (2) the phenotypic location of the actual potential mate under consideration. Beyond the *critical generalization distance* determined by the choosiness gene, this probability of mating goes to zero (see Fig. 1).

The choosiness gene actually encodes this critical generalization distance; typically, the larger this distance, the greater will be the number of individuals eliciting a positive probability of mating, so the less choosy the individual. Conversely, greater choosiness corresponds to a smaller generalization distance and to a taller, narrower mating probability function. Furthermore, we normalize the area under the mate preference function so that lower choosiness and wider generalization regions will not yield proportionally greater numbers of mating possibilities (otherwise every individual might evolve minimal choosiness and maximally large generalization values).

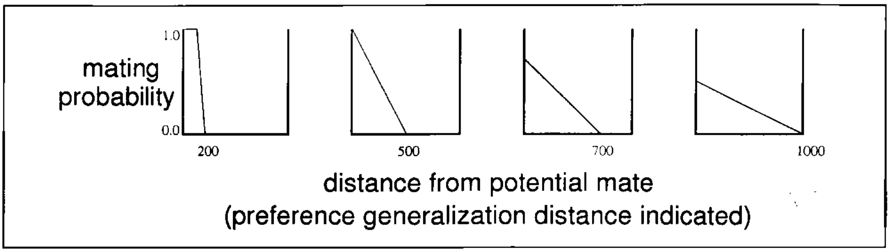

Figure 1
The area-normalized mating probability function.

As we are not interested here in how the choosiness parameter evolves, this normalization method seems justifiable.

The interaction between our area normalization technique and the otherwise linear falloff of the mate preference function can generate probabilities of mating greater than 1.0 when the generalization distance is very small and the mate preference function, as a result, is very tall and pointy; in such cases, we simply say that the mate is definitely accepted. Thus, for each individual in the population, we can visualize a cone-shaped surface swept out circularly by its mate preference function, sitting atop the phenotype space and specifying the probability that this individual would choose to mate with another individual with a given phenotype. Nonetheless, one individual's choices do not ensure that mating actually will occur; two must be consulted on this issue, as we will see next.

4.3 Implementing sexual selection through mate choice

Implementing sexual selection with mating preferences is fairly straightforward. To create the next generation, a "mom" individual is first picked at random from the current population. (If natural selection were operating in this scenario, differential fitnesses would be imposed here to alter the probability of selecting different moms but, because our fitness landscape is flat, all potential moms are picked with equal probability.) As it takes two to tango, a "dad" is next selected from the population in the same way. (Individuals do not have a sex per se; how each individual is picked determines whether it plays the mom or dad role in each mating.) The phenotypic distance between each parent's ideal mate location and the other parent's actual location is computed (using the Euclidean metric in the two-dimensional toroidal phenotype space), and each individual figures its probability of mating with the other based on this distance and its individual mate preference function. The two probabilities are likely to be different: For example, the mom might like the dad more than the reverse, either because he is closer to her ideal than vice versa, or because she is less choosy than he, or both. This situation is shown in Figure 2, in which the mom's

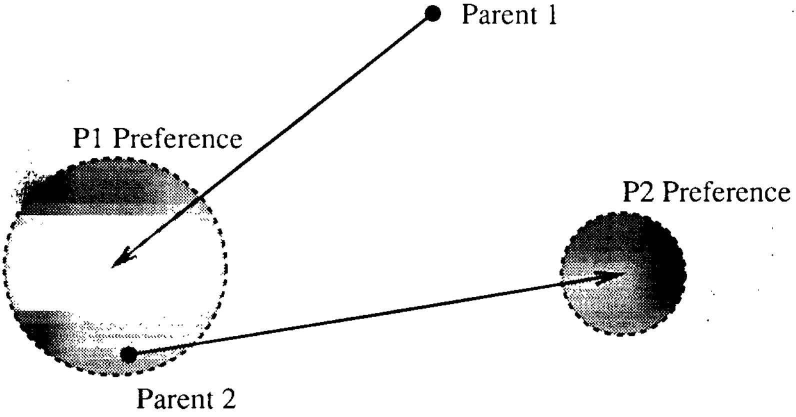

Figure 2
Two individuals and their mate preferences. Here potential parent 1 ("mom") would like to mate with potential parent 2 ("dad"), because he lies within her mate preference generalization region, but potential parent 2 will reject 1 because she is outside his generalization region.

preferences include the location of the potential mate dad, but the mom herself falls outside the dad's generalization region around his own ideal mate preference.

To accommodate this possible difference of opinion between the two potential parents, we multiply their probabilities together to yield a single probability that this pair will mate. Multiplying the two probabilities gives equal weight to each individual's choice in the matter, and mating happens only if both want it. Given this product, a die is thrown, and if their number comes up, the pair is mated. They are crossed over in the usual genetic algorithm manner (using two-point crossover), and the resulting offspring are put into the next generation. If the die roll fails, then a new dad is again chosen at random (with replacement), and the process is repeated, until the initially selected mom finds a mate. Once the mom mates, a new mom is picked (with replacement), and the search for a suitable dad begins again. This process, with a mom-selection loop wrapped around an inner dad-selection loop, continues until the next generation is filled. If a mom cannot find a suitable mate after five times through the population (i.e., after 500 mating attempts for our population size of 100), she is deemed hopelessly picky, and a new mom is chosen. Thus only those individuals who are sexually selected will be genetically represented in the next generation, and because this sexual selection is not female choice or male choice exclusively, it acts as a universal and pervasive force on every individual in our evolving populations.

The moms-sample-dads reproduction scheme we introduce here is unbiased in the sense that as a sampling method, it tends to preserve the frequency distribution (and the variance in that distribution) of phenotypes from one generation to the next. It allows different phenotypically separate and reproductively isolated clusters to maintain their relative numerical proportions by tending to pick mating pairs in just those proportions. This is important in promoting the speciation we will discuss in section 6. In contrast to our method, a random-pair sampling scheme, in which a mom and a dad are picked independently and randomly at each step and thrown back if they don't like each other, will bias the next generation's frequency distribution of phenotypes toward currently more common phenotypes. Smaller, reproductively isolated phenotypic clusters would be at a great disadvantage, because there would be a much lower probability of choosing both parents from the same small cluster simultaneously, so potential new species would be eliminated prematurely. Thus, under our sampling scheme, whatever evolution occurs can be attributed either to genetic drift or to sexual selection, not to a statistical artifact of the reproductive sampling.

4.4 Further simulation details

We use traditional bit-wise mutation (with a mutation rate of 0.01 unless otherwise stated) and two-point crossover. The crossover rate is 1.0—the mom and dad always cross over—because obligate sexual recombination is called for with our sexual selection scheme. To allow fairly fine-grained structure to emerge in the phenotype space, we use 15 bits to encode each trait and preference gene, 30 bits for the choosiness gene, and a single bit for the learning gene, yielding a total genotype length of 91 bits. (Because mutation and genetic drift can obviously have a substantial effect on the one-bit learning ability gene, we were careful to run controlled experiments with and without sexual selection, to disentangle the effects of drift from the effects of selection, as described later.) Population size for all runs in this article is 100 individuals.

Because natural populations usually form a cluster somewhere in phenotype space, restricted to a small range of the total possible phenotypic variation, it would be inappropriate here to start with a random initial population uniformly distributed throughout the entire phenotype space (the default for most genetic algorithm applications). Instead, we give the initial population some phenotypic elbow room into which it can branch out by starting it as a small random cluster in the middle of a much larger space of potential phenotypes. The entire space, as we mentioned earlier, is a 1000 × 1000 grid; initial trait genes are constrained to code for x and y phenotype traits in a range from 450 to 550, and the initial choosiness genes were constrained to code for generalization distances in a range from 100 to 200, to cover this phenotype range closely. This initial population (and all later generations) can be graphically displayed in a square grid with a dot at each individual's (x, y) phenotype position, an arrow leading from that location to the individual's ideal mate location, and a circle centered at the ideal with a radius equal to the individual's generalization distance, as shown in Figure 2 for just two individuals. Figure 3 shows such a representation for every individual in generation 0, with the centered square of initial phenotypic positions overlaid by the arrows and overlapping halos of the population's generalization regions (the arrows are not visible in this figure but can be seen clearly in later figures in this article).

Simulation Results

We can monitor the evolution of one of the populations in this study by watching how the individuals and their preferences shift around in phenotype space over successive generations. With no sexually imprinting learners in the population, only evolved and inherited preferences, we see the initial central blob (in Fig. 3) remaining mostly stationary in the center but jiggling and shifting a bit as the result of crossover and mutation (and more so with greater mutation rates). Occasionally, lone individuals are spat out into the surrounding phenotype space, but they usually find nobody else willing to mate with them and so die without leaving any offspring. The entire

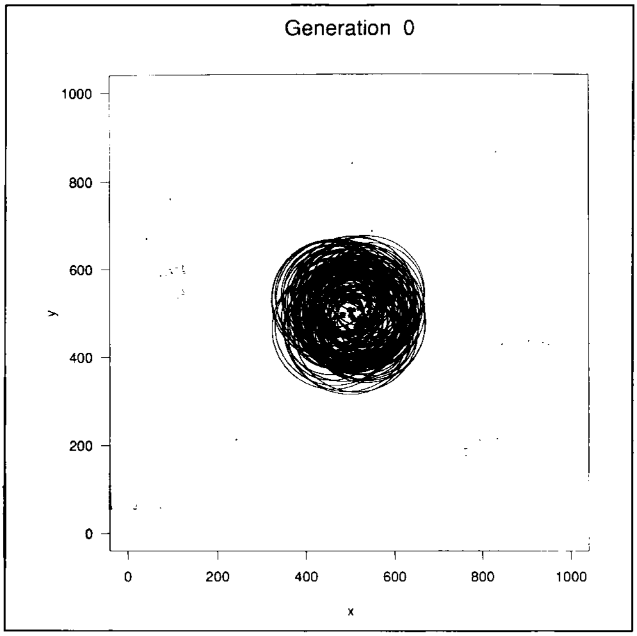

Figure 3
Graphic representation of the initial generation.

population may drift somewhat over many generations, ending up off-center (but remember that the center is not privileged over any other location). At this level, though, the population dynamics with evolved preferences generally look rather sluggish and uninteresting. (We will return to this question of macrolevel population behavior and illustrate these features in Figure 6, when speciation is discussed.)

5.1 Imprinted preferences help in finding mates

We can measure more subtle aspects of this evolution to get a better handle on what's happening. One useful statistic is the average number of attempted matings that it takes an individual to find an acceptable and accepting mate. This is computed by adding up the total number of attempted matings (moms sampling dads) that were required for one generation to fill up the population for the next generation, and dividing this number by the population size. (The mating attempts of the completely unsuccessful moms—those that fail to find a mate after 500 tries and are cast back into the pool as hopeless—are not included in this average, as we are interested here only in those individuals who *did* contribute to the next generation.) This measure represents the average difficulty that an individual had in finding a suitable mate—that is, in finding a phenotype that fulfilled his or her preferences and whose preferences were fulfilled by his or her own phenotype. By comparing average mating attempts per individual in populations that imprint versus populations that do not, we can determine whether sexual imprinting helps individuals find mates.

If we force the population not to use learning (clamping all the learning genes off) but to rely on evolved mate preferences instead, then we see 3.57 average mating attempts per individual, computed from data covering 10,000 generations (and thus 1 million individuals). This means that, on average, each mom had to search through approximately seven dads before a compatible mating pair was formed (twice the per-individual value to take both parents into account). If instead we force the population to use learning (clamping the learning genes on), then we see 2.44 average mating attempts per individual, again averaged over 10,000 generations. The latter case, 2.44, is significantly lower than the former case, 3.57 [$t(19998) = 33.74$, $p < .0005$]. In addition, the number of *failed* moms is significantly lower in imprinting populations than in inheriting ones, by nearly 50 percent. Thus learning is indeed making it easier for individuals to find appropriate mates. In our simulation, this difference in ease of finding mates will not result in differential genetic representation in the next generation because all these individuals *do* eventually get to have offspring (as we were including only the successful nonfailing ones). Only the complex sexually selective interactions between the traits and preferences of the moms and the dads drive evolution here, rather than the search costs for moms of finding mates. Nonetheless, the increased search efficiency allowed by parental imprinting could certainly matter in natural settings, as those individuals who can find suitable mates more quickly may get to have more mating opportunities and thus more offspring. This search efficiency may be another adaptive benefit of parental imprinting.

5.2 Imprinting is selected for

Having found this difference between populations of all-inheriters and all-imprinters, the next question is whether sexual imprinting will evolve in a population that begins without imprinters. To test this, we initialize a population of nonlearners (all having the learning gene set to off) and start it cycling through generations. This time the learning gene is allowed to evolve normally through mutation and sexual selection and determines whether the mate preferences are inherited or imprinted, as described in the previous section. Now if we monitor the frequency of the imprinting allele (i.e., individuals whose learning gene is on) as the population evolves, we can see whether sexual imprinting will indeed prove adaptive and spread through the population. As illustrated by the four sample runs shown in Figure 4, the answer is affirmative.

Because our learning gene is just a single bit, we need to be sure that the rise in the number of learners in the population is not simply due to genetic drift affecting that one-bit gene. To show that this gene is actually evolving in a directed fashion, we need to test whether it spreads through the population in this scenario faster than it would if

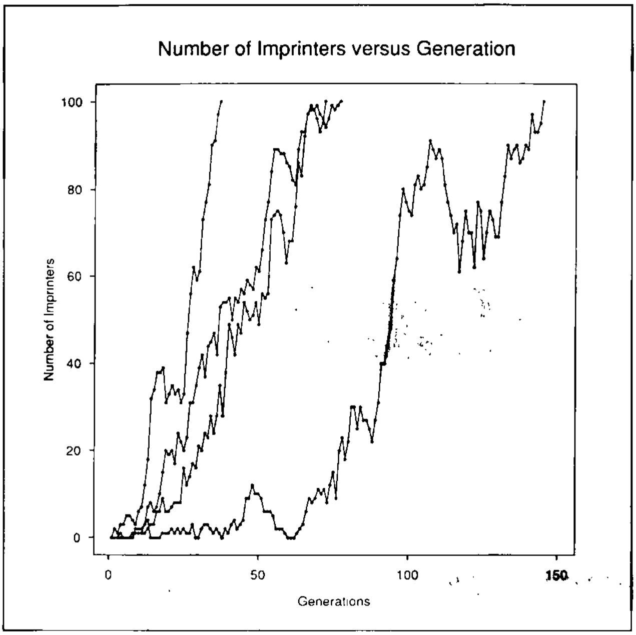

Figure 4
Number of sexual imprinters versus generations, showing steady upward evolution of imprinting, for four runs beginning with no imprinters.

it had no effect on the creatures—that is, if it were just junk DNA that would change in frequency according to random genetic drift. We can test this simply by comparing the average number of generations it takes for the learning genes to converge to 100 percent on[6] with the number of generations it takes to get there when it is not used (i.e., when it does not affect mating behavior and merely drifts). For each case, with and without selection on the learning gene, we ran 20 populations and recorded the number of generations it took the imprinting allele to reach 100 percent frequency in each; if it had not reached 100 percent by 999 generations, that number was used instead. With selection on the learnability gene, it took an average of 126 generations to reach 100 percent on, whereas without selection it took an average of 523 generations, which are indeed significantly different results [$t(38) = 5.12$, $p < .0005$]. This indicates that imprinting is in fact evolving in a rapid and directed manner. (We could get around the problem of worrying about learning that arises from random drift by using a more complex learning mechanism, or at least a more complex genetic representation of learning, so that the likelihood of the required set of coadapted genes appearing simultaneously at random would be greatly reduced. This was the case in our previous studies of the evolution of learning using neural

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[6] Note that the gene is not permanently fixated when it reaches 100 percent or 0 percent, because mutation and sexual selection can still drive it away from these boundary states.

network models [Todd & Miller, 1991a, 1991b], in which it was highly unlikely that a functioning neural network capable of adaptive learning would evolve purely by drift.)

5.3 Imprinting helps both parents mate

Now that we have concluded that sexual imprinting learning is steadily evolving in this population, we must return to the question of how this is occurring. What makes imprinting adaptive? Surprisingly, part of the action is in the individuals who never get to mate, those individuals who, in the mom role, proved hopelessly picky or unattractive and failed to reproduce even after 500 mating attempts. Because the moms are selected at random from the parent population, we would expect the proportion of imprinting moms who reproduce to match the proportion of imprinters in the parent population as a whole *if* none of the moms failed in their attempts to find a mate: That is, we would expect the number of imprinting moms in one generation to match half the number of imprinters in the previous generation (as moms make up only half the population). However, when we compare these two numbers, we find that imprinters are slightly but significantly more common in the set of moms who successfully reproduce than random sampling from the previous generation would have produced, by approximately 0.3 individuals per generation [$t(2026) = 4.82$, $p < .0005$].[7] The reason is that a disproportionate number of the nonimprinters that were selected as moms failed to find any mates and so did not make it into the next generation. Over 2027 generations (encompassing 20 runs of variable length), the number of nonimprinting moms who failed to find a mate was 1806 (occurring in 971 separate generations), whereas the number of failed imprinting moms was only 434 (occurring in 308 separate generations). Thus the imprinting moms succeed in finding mates more often than their nonimprinting competitors (that is, they fail less often), and so they are overrepresented in successive generations.

Nonetheless, the genes from the moms account for only half of what gets into the next generation. The selected dad individuals complete the other half, and the dads, too, add a disproportionate number of imprinters compared to the previous generation [approximately 0.6 new imprinters per generation; $t(2026) = 10.88$, $p < .0005$]. The dads get into the next generation based just on how well their own preferences match the phenotypic locations of the moms and how well they match the preferences of the moms, but their imprinting affects only the former. This indicates that imprinters do, in fact, have mate preferences better adapted to the evolving population structure, accounting for their ability to take over the population

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[7] Here again we have analyzed 20 runs beginning with no imprinters and have stopped whenever they reach the point of all being imprinters or pass 999 generations.

as evolution progresses. Because the sexual selection of individuals in the mom role accounts for 0.3 new imprinters per generation, and selection of individuals in the dad role accounts for 0.6 new imprinters per generation, we can conclude that imprinting is favored through both channels. Because moms are repeatedly sampling dads under our reproduction scheme, we would expect the selective pressures on dads to be higher, accounting for this twofold difference.

5.4 Imprinting evolves to track current phenotypes

Moving from the mechanism underlying this evolution, we can proceed to explore the evolutionary function of sexual imprinting. The adaptive function of sexual imprinting may be described as tracking phenotypic variations in a population over time. These variations are caused by the forces of mutation and crossover, creating new distributions of phenotypes from one generation to the next. But if sexual imprinting evolves to track phenotypic change, what happens when the rate of that change itself varies? We hypothesized that very slow change across successive generations would give imprinting no advantage over inherited preferences, while very rapid change would overwhelm the ability of imprinting to keep up. We realized that here was another case of a U-shaped relationship between the time to evolve a form of learning and the noisiness of the environmental signal on which learning relies, the same sort of relationship we found earlier in our studies of both the evolution of associative learning (Todd & Miller, 1991a) and sensitization and habituation learning (Todd & Miller, 1991b; see also Littman & Ackley, 1991, for a similar result). In this case, the environmental condition that individuals must track is the current location of the population in phenotype space. The cue that an imprinting individual uses as an indication of that information is the phenotypic location of its own parent(s), and the noisiness of that cue corresponds to the mutation rate of the evolving population. High mutation rates tend to disturb the correlation between cue (parental phenotype) and environmental condition (population average phenotype), because each parent is more likely to have been mutated away from the population average. Thus, by manipulating mutation rate, we manipulate the correlation between perceptual cue and environmental condition on which learning depends.

Based on the same logic used in our previous studies of the evolution of learning (Todd & Miller, 1991a, 1991b), we hypothesized that imprinting would prove most useful and evolve most quickly at intermediate mutation rates. The plot in Figure 5 shows that our suspicions were correct. Here we have controlled the effective rate of phenotypic change in the population by varying the mutation rate, from 0.0 to 0.1. The values plotted for comparison at the far right actually come from the random-walk case where the learning gene is not used and so is subject only to drift. We also seed the initial population differently in this case: Rather than begin with a population

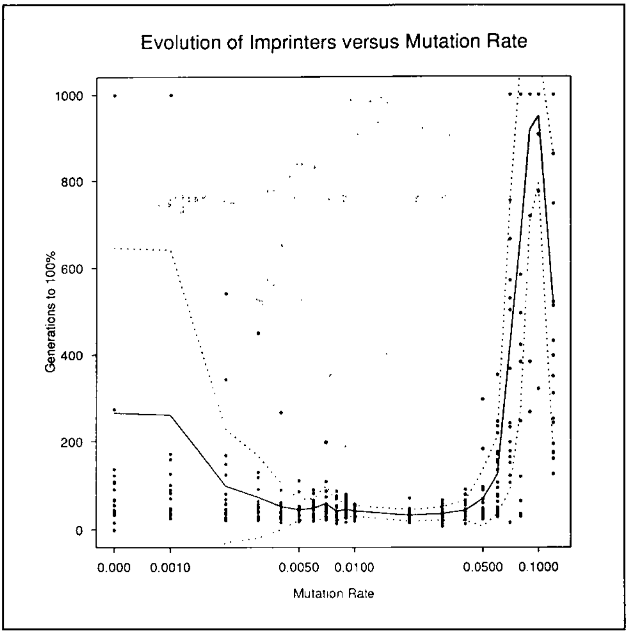

Figure 5
Number of generations to evolve sexual imprinting versus mutation rate. Dots are data points from 20 runs; mean values are indicated by the solid line; and standard deviations around the mean are indicated by the dashed lines. The mutation rate varies from 0.0 to 0.1, in steps of 0.001 from 0.0 to 0.01, and in steps of 0.01 from 0.01 to 0.1. The *x*-axis is transformed logarithmically (but with mutation rate 0.0 added at the far left) to allow the small mutation rates to be seen more distinctly. The values for the random-walk case (no selection on the learning gene) are shown at the far right.

containing no imprinters, we start with a population containing half imprinters (50) and half nonimprinters (50). If we started with no imprinting individuals, the evolution of imprinters would be artificially impeded by the slow introduction of imprinting alleles at the very low mutation rates. We graph the number of generations taken to reach 100 percent imprinters in the population, or 999 generations if the population has not reached 100 percent by then. As expected, the average number of generations to evolve imprinting (indicated by the solid line) follows a U-shaped curve, growing large toward the extremes of high and low variation (mutation rate) and small for middling values. (Note that a longer time to evolve imprinting signifies a lower adaptive value for learning; conversely, where the time to evolve imprinting is lowest, at the intermediate mutation rates, its adaptive value is apparently highest.) We account for this U-shaped curve as follows.

5.5 Benefits of imprinting depend on mutation rate

For a wide intermediate range of rates of phenotypic change in the population (corresponding to intermediate mutation rates), sexual imprinting can usefully track the phenotypic variation from one generation to the next. Parents will spread around in phenotype space from generation to generation but not by too great a distance at once, and they will tend to have offspring who end up in phenotypically nearby locations since the mutation rate is not exorbitant. Therefore, if their offspring imprint on the phenotypic locations (i.e., appearances) of the parents, those offspring are likely to find suitable mates (other offspring of other similar parents) at nearby locations in the next generation. If the offspring continue to use evolved, nonimprinted preferences instead, they could be left behind as the population shifts to a new region of phenotype space. Thus imprinting proves adaptive at medium levels of phenotypic variation and will evolve relatively rapidly.

If, however, the mutation rate is very low, leading to little phenotypic variation from one generation to the next, then an evolved preference will suit individuals fairly well because the population is unlikely to move about in phenotype space. Imprinting thus takes longer to evolve because it offers little, if any, additional advantage. Moreover, a learned preference could be a hindrance in this case, particularly when parents end up separated from the main population cluster by a rare mutation and wind up raising offspring with similarly skewed mate preferences who thus will have little hope of finding a suitable mate. However, this negative effect is apparently not strong enough to select against imprinting at low mutation rates; imprinting still evolves faster than in the purely random drift case shown at the far right of the plot. (In fact, at 0.0 mutation rate, imprinting might allow individuals to track the inevitable convergence of the population more rapidly than evolution can, by using the parental phenotypes as an indication of where that convergence is heading; this case remains to be investigated.)

High mutation rates are yet another story. Above nearly 0.06 mutations per bit per generation, there is more ongoing variation in the population than imprinting can reasonably track. Under these conditions, parents in one generation generally will have offspring that are quite dissimilar from them in the next, so the phenotypic location where one's parents were is less likely to yield many potential mates in the current generation. Thus imprinting proves less valuable and takes longer and longer to evolve with increasing mutation rates. Evolved preferences are not much use either for population tracking under high mutation rates, because evolution would have little chance of converging on any appropriate phenotypic preferences before the population had evolved off to somewhere new in phenotype space.[8] Still, at the highest mutation rates, evolved mate preferences seem to be more adaptive than

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[8] In fact, both imprinters and inheritors have a much harder time finding mates under high mutation than under low mutation. We can see this by determining the average number of mating attempts (dads that have to be tested by each mom) before an acceptable pairing is consumated. With a mutation rate of 0.03, an average of 10.4 mating attempts over 500 generations are required before success; with a mutation rate of 0.08, this value rises to 28.1. (In contrast, with a mutation rate of 0.0, finding a mate is very easy, with only 0.72 mating attempts on average. This is because the population quickly converges to a steady state, which the evolved or learned mate preferences can easily match.) Of course, a different kind of mate choice mechanism capable of sampling many individuals from the current population, and computing a mean current phenotype as the preference, could largely overcome this problem of high mutation rates.

imprinting, because imprinting takes longer to evolve to 100 percent then than in the random-walk case, indicating that it may be slightly selected *against*. The likely explanation here is that the population density is generally lower with higher mutation rates, so parents on the outskirts of the population's phenotypic distribution will not provide very good targets for their imprinting children as there won't be many other individuals around. Children who inherit preferences for the center of the population distribution (however diffuse) will at least have a few more potential mates to choose from in the next generation.

5.6 Imprinting may affect phenotype change

It begins to appear that sexual imprinting can evolve in a somewhat circular way. As we have just shown, this type of learning can be adaptive when the population is evolving at a moderate rate because it tracks population changes and gives individuals better mating opportunities. In addition, imprinting may foster the very change that selects for it, because mate preferences that update themselves each generation through learning could make the population move more rapidly and fluidly through phenotype space. If this is so, it may be a bit of a chicken (or snow goose) and egg problem of which comes first, population change sped up by imprinting or imprinting to track that change. Either way, once imprinting begins to invade the population, its occurrence could self-catalyze: A few imprinters would allow the population to change a bit more rapidly, which in turn makes imprinting a bit more useful in tracking that more rapid change, which in turn selects for more imprinters, and the frequency of the learning behavior could ratchet higher and higher.

Just what kind of population movement does parental imprinting allow? We thought, at first, that imprinting would help a population to track a moving fitness peak of the sort that could arise in coevolutionary situations. This does not appear to be the case, however. In preliminary experiments, we have added to our model natural selection in the form of a fitness peak that slowly moves around phenotype space along a straight or circular path. To our surprise, we found that populations of imprinters were uniformly less able to keep up with the moving fitness peak across generations than were populations with inherited mate preferences. Preferences that always pointed back to the phenotypic locations of parents in the previous generation were generally maladaptive once the fitness peak had shifted in the current generation. Instead, we believe that imprinting may be best at tracking population shifts between already existing morphs—that is, shifts in the relative frequencies of different phenotypes such as the two color phases of the snow goose. In such cases, the parent-based preferences generally remain appropriate from one generation to the next and may help track changes in the relative fitnesses of different morphs due to changing environmental conditions. This expectation is more in line with those of Seiger (1967; Seiger & Dixon, 1970), that imprinting will tend to limit a population to already existing morphs by rendering new mutants undesirable. We continue to explore these issues in the hope of better understanding how different mate choice mechanisms can track and facilitate population movements through phenotype spaces.

6 Sexual Imprinting and Speciation

We have just seen that imprinting can evolve in a population to facilitate individual mate selection. But what has the population itself been doing in phenotype space all this time? As we indicated in previous sections, sexual imprinting can have more than just adaptive effects at the individual level. Imprinting can also have important effects on the structure and evolution of the population as a whole, often leading to speciation, the splitting of the population into phenotypically isolated subpopulations between which mating rarely occurs. Speciation is one of the most important of macroevolutionary phenomena, leading to the variety of life we find on our planet today. That individual learning can have an effect on such a major population-level process clearly shows the importance of psychological mechanisms in the biological realm.

6.1 Sympatric versus allopatric speciation

Our sexual selection model presented here demonstrates the viability of *sympatric* speciation, the splitting apart of a geographically coherent lineage into reproductively isolated populations without the intervention of spatial barriers to mating (*sympatric* means "same fatherland"). The most widely accepted theory of speciation, Mayr's (1942) *allopatric* ("other fatherland") model, denies the likelihood of such sympatric speciation: Geographical features such as mountains and rivers (or just being on different geographical margins of a parent population) are seen as the primary forces that split populations apart. In the allopatric model, once the initial isolation of subpopulations occurs, their tendency to drift genetically further apart will eventually make them incapable of interbreeding, and speciation is complete. Dobzhansky (1937) advocated the possibility of sympatric speciation but proposed that it would rely on an analogous splitting force: a low-fitness valley between separate fitness peaks in an "adaptive landscape" (Wright, 1932). Populations would thus split to occupy the separate econiches represented by the adaptive peaks, between which disruptive natural selection would make interbreeding maladaptive. In contrast to both of these speciation mechanisms, our model of sympatric speciation (originally described in Todd & Miller, 1991c) requires neither spatial restrictions on mating nor any natural selection at all: speciation happens on a geographically undifferentiated flat fitness landscape. Rather, we rely on the evolution of individual mate preferences via sexual selection, which serve to isolate subpopulations *reproductively*. (We have dubbed this the *Quicksilver model*, after the way species split off due to random jiggling forces in the same way that blobs of mercury split when shaken, yet remain coherent subblobs afterward.)

6.2 Previous ideas about sympatric speciation through imprinting

Sexual imprinting is one example of a mate choice mechanism that tends to induce speciation (see Todd & Miller, 1991c, and Miller & Todd, 1993a, for a discussion of others). Imprinting has long been proposed as a possible mechanism by which new species could be formed, with the following reasoning: imprinting can promote assortative mating, which in turn can lead to polymorphism, and then to the eventual isolation of different morphs into new noninterbreeding species.[9] Kosswig (1947, 1963) suggested imprinting as a possible explanation for the rapid speciation that produced the unusual diversity of cichlid species in East African lakes, and Cushing (1941) hypothesized that it could have a similar evolutionary effect in birds. These proposals were not empirically tested until recently, when researchers have begun to study the possibilities of imprinting and speciation in fish (with mostly negative results—see Barlow et al., 1990, and Siepen & Crapon de Caprona, 1986) and in finches (with a more positive appraisal—see Grant & Grant, 1979, and Immelmann, 1975).

Convincing empirical proof is still needed, but mathematical and computer simulation models (Kalmus & Maynard Smith, 1966; Seiger, 1967; Seiger & Dixon, 1970; O'Donald, 1960) have shown that sexual imprinting can theoretically lead to stable polymorphism and speciation. In particular, Seiger (1967) and Kalmus and Maynard Smith (1966) implemented mathematical models of a single-locus two-allele case. Both studies found that absolute imprinting (in which all individuals imprint) could engender separate noninterbreeding species, whereas partial imprinting (only some portion of the population imprints) could yield a stable equilibrium consisting of a balanced phenotypic polymorphism in the population. Seiger (1967) further argued that a single allelic difference, as used in his model, could realistically account for speciation. Our model supports these findings and extends these ideas to a multilocus, continuous-allele genetic system. Furthermore, we allow the prevalence of imprinting itself to evolve along with the phenotypic traits rather than evolving just those traits alone. These added complexities make our scenario even less mathematically

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[9] Indeed, Mayr (1947), in an early attack on sympatric speciation, reports that homogamy—positive assortative mating—was originally believed to be the main cause of speciation when blending theories of inheritance were prevalent; without homogamy, the genetic diversity necessary for speciation would be eliminated through blending. Mayr goes on to deny assortative mating as a reasonable mechanism for speciation, a position which seems less tenable today.

tractable than the earlier ones, so that simulation is really the only feasible way to explore its implications.

6.3 Imprinting facilitates sympatric speciation in our model

In our model, a species appears as a cluster of individuals in phenotype space, all having mate preferences centered on or near that cluster.[10] We begin our simulations with a single initial species, as shown in Figure 3. From there, different things can happen to the population, depending on the types of mate preferences implemented. First, if we allow only evolved mate preferences, then the population tends to be fairly stable, as we described earlier. It may drift slightly from its initial central position and may spit out mutant individuals from time to time, but in general it will remain a single species, sometimes getting even more tightly clustered in phenotype space (provided the mutation rate is not too high; here and in the following run we use a mutation rate of 0.005). This phenomenon can be seen in the view of a typical population over several generations, depicted in Figure 6, which shows the locations of the individuals in the population along with their preferences and generalization regions. In generation 10, we see the initial cluster, with one individual's choosiness gene mutated to create a very large generalization distance (the large circle extending off the edges of the plot). This central cluster remains intact for the 700 generations we have shown here, growing a little tighter over time as evolution discovers that choosier individuals fare better at finding mates. At generation 50, we see a couple of individuals spat out from the central cluster but with preferences pointing back into that cluster, and we also see one individual inside the cluster whose preference has mutated to lie outside. All three of these individuals will be unable to find acceptable or willing mates and so will not have offspring in the next generation. At generation 200, a few more individuals and preferences have mutated away from the majority of the population. There is even the beginning of a small potential species at the far right edge, but this is short-lived (though another attempted species reappears at this location in generation 500). Overall, though, the original central species holds sway, shifting slightly "eastward" by generation 700 but remaining largely stationary and coherent. Evolved mate preferences can thus be interpreted as a somewhat conservative force, tending to keep the population together phenotypically by dampening population movement and splitting.

Learned mate preferences, sexually imprinted from the parents, lead to very different results. If we look at a population with all imprinted preferences, we see relatively

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[10] Note that we are not wedded to a particular definition of *species* in this research program (see Ereshefsky [1992, pp. 5–13] for a review of species concepts). However, because we rely on phenotypic clustering (as well as minimal interbreeding), Cracraft's (1992) phylogenetic species concept may be particularly appropriate. Wiley's (1992) evolutionary species concept is also appealing given our adaptationist outlook.

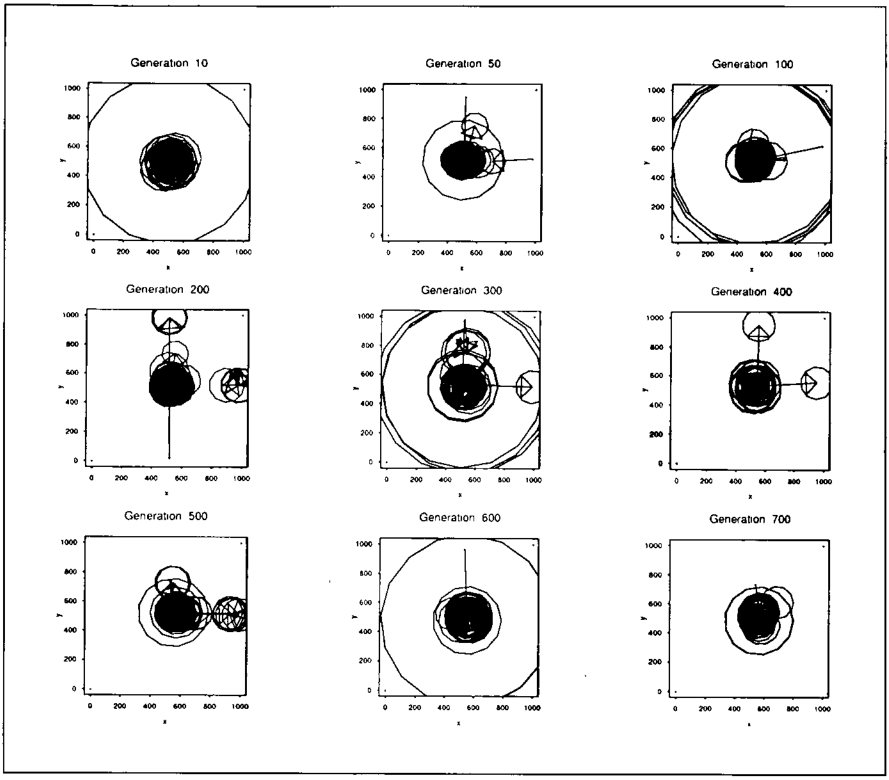

Figure 6
Population dynamics with evolved (inherited) mate preferences over 700 generations.

frequent speciation events, as shown in Figure 7. Here we can see species splitting off at generations 100 and 500, with only one species winning out and surviving in between, probably because of our fixed population size. (If we were to allow the more natural possibility of expanding populations, species would not be in such direct competition with one another and could survive longer.) Furthermore, the population as a whole moves around in phenotype space considerably more than in the evolved-preference run in Figure 6. Finally, the species clusters are, for the most part, more tightly clumped than with evolved preferences because of greater evolved individual choosiness. This probably allows smaller changes in the distribution of population phenotypes and preferences to lead to the isolation and splitting off of new species, compared to the changes necessary to overcome the cohesive force of evolved preferences and cause speciation in that case.

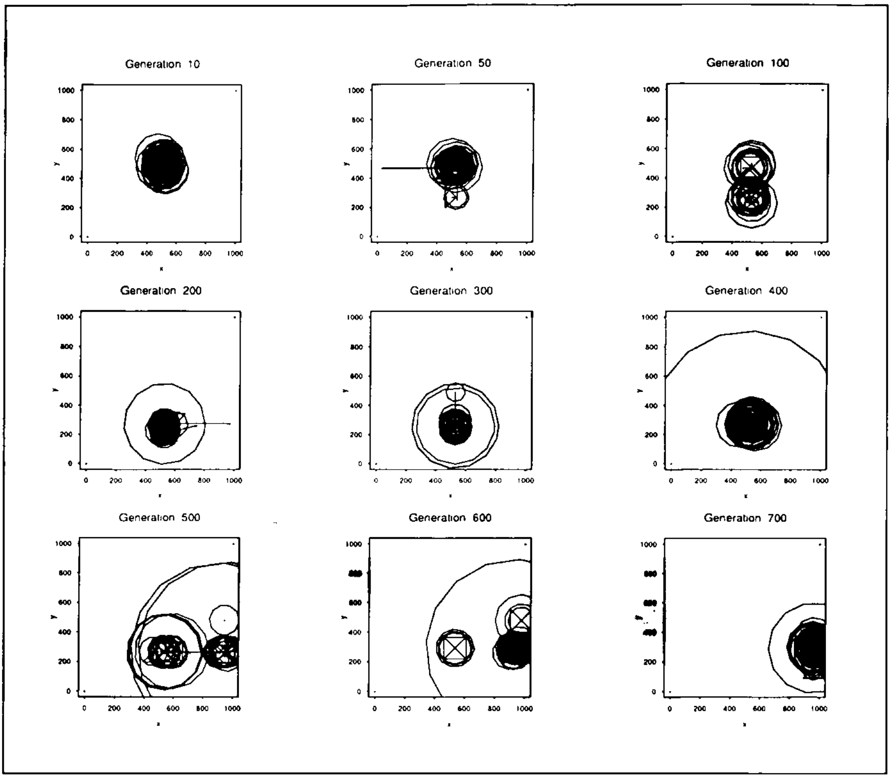

Figure 7
Population dynamics with learned (imprinted) mate preferences over 700 generations.

6.4 Selection for rates of speciation?

We are exploring the use of clustering methods to quantify the amount of speciation occurring in our simulations. Preliminary analysis of many simulation runs indicates that speciation is approximately three times more common in imprinting populations than in nonimprinting ones. This suggests that sexual imprinting functions at the population level as a more fluid, less conservative adaptive force, keeping single populations in cohesive clusters that are more susceptible to being split by the random jiggling forces of mutation and crossover. Once the newly split species begin to diverge in phenotype space, sexual imprinting will again tend to consolidate each cluster, keeping individual mate preferences local so that little interbreeding will occur between the subpopulations. The clusters will then continue to drift farther apart until they are reproductively well isolated, effectively constituting new species. Over continuing time in our simulations, separate species may rejoin into one because of the limited phenotypic range over which they can vary, but in more natural situations, this rejoining is unlikely to occur because drift and selection will operate on a vastly greater number of phenotypic traits to reinforce the divergence between populations, once reproductive isolation is in place.

Based mainly on empirical findings rather than simulation results, Immelmann (1975, pp. 248–249) has proposed that the main function of sexual imprinting may, in fact, be to facilitate speciation:

> Altogether, it can be concluded that early experience has two possible evolutionary functions: initially it leads to the formation of habitat and other ecological preferences in any one individual through environmental imprinting; as soon as natural selection has led to the evolution of slightly different gene-pools adapting groups of individuals to local conditions, it also serves to preserve such gene-pools by means of sexual imprinting. . . . If genetical isolation between sub-populations becomes more and more complete, the ecological preferences that initially were based on early experience, together with sexual imprinting, will finally be able to initiate speciation.

Everything Immelmann says here would likely still apply even if the mate preferences were based on inherited (evolved) templates rather than learned ones, although speciation would probably take longer in that case. Our simulations do show that speciation is faster (i.e., more common) with learned preferences.

Our model also differs from Immelmann's scenario in that we can achieve speciation without any initial population differences due to natural selection. Research with *Drosophila* (Koref Santibanez & Waddington, 1958) has indicated that the sort of small initial differences in preferences that can lead to stronger isolation, and the speciation that we find, could indeed arise through stochastic evolutionary effects, just as they do in our model. However, if disruptive natural selection were added to our sexual selection, speciation would certainly happen much more rapidly.

Perhaps this ability to speed up speciation is, in fact, an additional adaptive function of sexual imprinting. Immelmann (1972, p. 167) has stated that "imprinting may be of special advantage in any rapidly evolving group, as well as wherever several closely related and similar species occur in the same region [i.e., sympatric situations]. Interestingly enough, both statements really do seem to apply to all groups of birds in which imprinting has been found to be a widespread phenomenon. . . " "Perhaps the occurrence of imprinting represents some sort of a pre-condition for rapid and extensive adaptive radiation, at least in vertebrates" (Immelmann, 1975, p. 250). Indeed, if we combine the finding that populations composed entirely of imprinters tend to speciate relatively frequently with the finding (from the previous section) that imprinting evolves and spreads through our populations, we can conclude that the *tendency to speciate* evolves in our model. In our case, speciation emerges as a side effect following the evolution of individually adaptive parent-imprinted mate preferences. However, in nature, if Immelmann is correct, the ability to speciate could sometimes prove so adaptive that it imposes higher-level (e.g., species, genus, etc.) selection for imprinting.

This is a tricky argument but is less implausible than it might first appear. Species-level selection may be one of the few viable options for explaining why sexual recombination persists at all (Williams, 1975; Maynard Smith, 1978). If the enormously complex machinery of sexual reproduction and sexual recombination is itself maintained by species-level selection, then it is only a small additional step to suggest that selective mate choice mechanisms, which simply bias with *whom* one recombines, could also arise through species-level effects. Moreover, if mate choice mechanisms are, as we propose, among the strongest and most direct influences on speciation rates, such mechanisms should be among the biological traits most susceptible to species-level selection. Further investigation of such processes in large-scale computer simulation may illuminate the old debate over the units of selection in evolution (Brandon & Burian, 1984; Ereshefsky, 1992; Williams, 1966) and may demonstrate whether species selection can really affect mechanisms for individual adaptive behavior such as mate choice.

7 Implications and Further Research Directions

7.1 Imprinting and species category learning

Sexual imprinting, as we have seen, is a worthy subject of study in its own right, not just as an interesting adaptive behavior in the natural world but also for what it can tell us about the interplay between learning and evolution. Many other aspects of this phenomenon remain to be explored. One mystery, related to issues of category learning in cognitive psychology (see Harnad, 1987) is how individuals construct the perceptual category of traits or objects to which they are sexually attracted. This is particularly curious when the category corresponds to an entire, and different, species; as Lorenz (1935/1970, p. 246) put it, "It remains a complete enigma as to how the bird is able to zoologically 'classify' the species to which it erroneously 'feels itself to be related'." Shepard (1987a, 1987b, 1990) has been concerned to discover the universal laws by which animals generalize and categorize stimuli to guide their behavior adaptively. Because selective mate choice mechanisms make species uniquely self-defined as "natural kinds," and because species are probably the most important categories of objects about which animals should learn (to know what to eat, what to flee from, and what to mate with), innate predispositions to classify organisms into species should prove adaptive. Such species-category predispositions may underlie the universal generalization and categorization laws Shepard seeks. Experimental studies of cross-species imprinting should be helpful in investigating this area, by providing a clear window onto the formation of species concepts. (In fact, Spurway [1955] even suggested that imprinting could be the basis of biological taxonomy, in humans and in other species.) Studies of more specific imprinted categories, such as those that focus on close kin (Bateson, 1978, 1983; Ten Cate, 1987), may also inform the ongoing debate in cognitive psychology concerning whether category formation occurs through stored exemplars, computed average prototypes, or some other learning mechanism. By elaborating our model to include mechanisms of sexual imprinting and mate choice that allow more sophisticated category formation, we hope to address these and similar issues in the future.

7.2 Extensions to other mate choice mechanisms and selection schemes

Beyond parental imprinting, we have begun to explore a variety of other mate choice mechanisms. We are particularly interested in preferences that incorporate more complex social information sampled from many individuals rather than just one individual (e.g., the parent), as seen in the phenomena of preference copying and population averaging. In the former, individuals adjust their desires based on the observed preferences, rather than the phenotypes, of other individuals (see Pruett-Jones, 1992); in the latter, individuals sample some portion of the population and learn preferences to match the current most common (or fittest) phenotypes. In future work, we will compare the effects of different types of preferences on population evolution (convergence, drift, peak-tracking, etc.) in a variety of settings (flat fitness landscape, moving fitness peaks, changing morph advantages, etc.), both to increase our understanding of the biological situations and to look for useful properties for artificial evolution applications, as we will discuss briefly later. It will be of great interest to determine whether those mate choice mechanisms that tend to increase short-term individual fitness also tend to increase the long-term efficiency of macroevolution as a process of search and diversification.

We are interested as well in Fisher's (1930) theory of runaway sexual selection, which has recently received support from population genetics models (Lande, 1981; Kirkpatrick, 1982; Pomiankowski, Iwasa, & Nee, 1991) and computer simulations (Collins & Jefferson, 1992). We have explored the effects of allowing mate preference functions to evolve asymmetrical, directionally biased forms and have found that such "directional preferences" (Kirkpatrick, 1987; Ryan, 1990) can lead the population to careen capriciously around phenotype space in a runaway manner, displaying a kind of "evolutionary wanderlust" (Miller & Todd, 1993a). There are reasons to believe that the runaway process also works with nondirectional preferences (Gould & Gould, 1989), and we intend also to model this case in the future. Such simulations may prove important in psychology because we suspect that the tripling of brain size in our species over the last 2 million years may have been driven by runaway sexual selection operating in both sexes (Miller, 1993a).

Increasing the realism of our sexual selection simulations will allow us to model other important natural phenomena. At the moment, we have sexual selection among individuals that are not of separate sexes. To address this, we can make our individuals male or female throughout their lifetime (as most creatures are, not counting certain human subpopulations) rather than floating between mom and dad roles as they do now. This change will allow us to study the evolution of sexual dimorphism, which is a common, though not inevitable, result of sexual selection (see Lande, 1987). We anticipate that dimorphism may have complex effects on speciation, on how runaway sexual selection works, and on how populations escape from local evolutionary optima (Miller, 1993b). For example, dimorphism may make sympatric speciation more difficult, because an existing species would have to split apart into new population clusters that *each* contain sexually differentiated phenotypes. The complex effects of sexual differentiation on evolutionary dynamics, and vice versa, are difficult to study using analytical techniques, so computer simulation may prove invaluable.

Another major change would consist of our letting the population size fluctuate around some desired figure by giving each individual in a generation an equal number of mating opportunities. As before, only those who have appropriate preferences and preferred traits will be honored with mating opportunities and offspring in the next generation, but the numbers of those matings and offspring will not be arbitrarily limited. Relaxing this constraint should also facilitate speciation and the rise of biodiversity, in comparison with the fixed populations we now have, wherein the rise of one species typically entails the decline of another.

7.3 Reasons for simulating sexual selection

Sexual selection and mate choice have recently become among the hottest topics in biology and behavior. We believe that simulation models offer a very powerful, novel, and enticing means for advancing our understanding of these phenomena, and we wish here to emphasize some of the advantages of studying sexual selection with simulation methods. First, whereas mathematical population genetics models (e.g., O'Donald, 1980; Lande, 1981; Kirkpatrick, 1982) are limited to simple, formally tractable interactions, simulation models can make much weaker and more plausible assumptions, can implement much more complex and realistic mate choice mechanisms, can give rise to much more complex evolutionary effects ranging from the level of individual behavior to the level of macroevolution, and can more accurately reflect the stochasticity of evolution in finite populations (most formal models assume deterministic evolution in infinite populations). (See Collins and Jefferson [1992] for an elegant example of the power of evolutionary simulation in this regard.) Implementing a new mate choice mechanism in simulation simply requires changing a few lines of code, whereas writing down the formal recursion equations for evolution given a new mate choice mechanism may require completely rethinking the mathematics, which may suddenly prove intractable.

Second, sexual selection can often be simulated more easily and plausibly than natural selection, because each individual's environment is composed solely of the other individuals in the species; there is no need to develop complex models of real-world environments with food, predators, obstacles, and so on. This means that important biological principles of sexual selection can be explored with much simpler techniques than would be necessary in studying adaptation to econiches under natural selection.

Finally, people's intuitions about sexual selection tend to be poorer than those about natural selection. Thus, simulation as a method of doing computer-assisted thought experiments about sexual selection may be a particularly effective way to hone our intuitions about these complex and counterintuitive evolutionary processes. In this way, simulation models of sexual selection can provide plausibility checks on new hypotheses before they are put to empirical test, and can suggest new phenomena to look for that might not otherwise have been discovered.

Simulation models are also inherently flexible, in both assumptions and interpretation. For example, the model we have presented here can easily be extended to simulate allopatric situations, rather than sympatric ones, by interpreting the two-dimensional phenotype space as a two-dimensional geographical space. With such a shift of viewpoint, parental imprinting becomes habitat imprinting, preference regions become home territories, the random effects of mutation and crossover become dispersal, and population motion through phenotype space becomes migration. Thus our model can have a wide range of implications for allopatric speciation and geographically induced macroevolutionary changes as well.

7.4 Combining natural and sexual selection

Additional phenomena of interest can be explored when we add natural selection to the sexual selection scenario we have developed here. One might expect strong natural selection pressures to swamp any sexual selection effects on speciation or learning. However, we have found that when the phenotypic dimensions on which natural and sexual selection impinge are different, rapid speciation can still occur and in such a way as to distribute the population to fill the available natural-selective niches. That is, from an original population, lineages can branch and diverge to climb different adaptive peaks and search the natural-selective fitness landscape in parallel. (We will report on this work elsewhere.) Nonetheless, natural and sexual selection can also disagree rather than cooperate: When we add directional mate preferences into the mix, sexual selection can cause happily converged populations at the top of fitness peaks to tumble back down them, leaving safety and survival behind in a mad-dash pursuit of sexual fulfillment (Miller & Todd, 1993a). Such evolutionary forays away from fitness peaks may often lead to extinction, but they may also help populations to escape local optima in phenotype space and find better peaks elsewhere (see Miller & Todd, 1993b).

Adding natural selection to our model opens the door not only to additional scientific uses but also to engineering applications. In the last decade, genetic algorithms and other evolutionarily inspired methods have been used as search and optimization techniques to solve problems ranging from gas-pipeline design to goods-shipment scheduling (see Goldberg, 1989). In such applications, the problem is interpreted as an adaptive landscape with different possible solutions having different levels of fitness, and the goal is to find a solution at a fitness peak in that landscape using processes analogous to natural selection. Sexual selection can play a powerful role here too. Mate preferences for traits that are uncorrelated with natural-selective fitness may enhance evolutionary search and species diversification, and mate preferences for traits that are correlated with natural-selective fitness may enhance evolutionary optimization and niche exploitation.

Specifically, as a process of search and diversification for exploring large, complex, high-dimensional adaptive landscapes in various application domains, sexual selection may (1) promote spontaneous sympatric speciation through assortative mating, increasing the number of reproductively isolated lineages performing the evolutionary search; (2) help populations escape local fitness minima because "directional mate preferences" (Kirkpatrick, 1987; Miller & Todd, 1993a) can confer a kind of evolutionary momentum on them; and (3) facilitate the emergence of evolutionary innovations through intrinsic perceptual biases (Ryan, 1990) in favor of morphological and behavioral novelty (which were observed by Darwin [1871]). The net result of these three processes is that sexual selection may be to macroevolution, in artificial search applications as in nature, what genetic mutation is to microevolution: the prime source of potentially adaptive heritable variation. Further, as an optimization process, sexual selection might (4) speed evolution by increasing the effective reproductive variance in a population even when survival-relevant differences are minimal, thereby imposing an automatic, emergent form of "fitness scaling" (Goldberg, 1989); (5) speed evolution by increasing the accuracy of the mapping from phenotype to fitness and thereby decreasing the "noise" or stochasticity intrinsic to many forms of natural selection; and (6) promote the elaboration of morphological and behavioral innovations before they become ecologically useful (e.g., through

Fisher's [1930] runaway process, thereby bringing populations into the region of new adaptive peaks). In collaboration with other researchers at the University of Sussex, we are currently exploring these possibilities, both through basic performance tests on N-K fitness landscapes as developed by Kauffman (1993) and through applications to the design of autonomous robots, turbine arrangements in jet engines, and fuselage and wing configurations for commercial aircraft (Miller, 1993b; Miller & Todd, 1993b). Further, insofar as runaway sexual selection was probably central to the evolution of the human brain (Miller, 1993a), simulating sexual selection may, at some future date, help researchers cross the border between artificial life and artificial intelligence.

Conclusions

We have shown in this article that learning in the form of parental imprinting can evolve solely through the effects of sexual selection rather than through natural selection, as is usually supposed. The adaptive function of this type of learning is to select suitable mates and thereby to ensure genetic representation in the generations to follow. Furthermore, we have found once again that the rate at which a learning mechanism evolves can be affected by the "noisiness" of the environmental cue that it employs. The relation of time to evolve imprinting versus mutation rate follows the same U-shaped curve discovered in previous studies of the evolution of learning (Todd & Miller, 1991a, 1991b; Littman & Ackley, 1991). Finally, we have seen that the evolution of learning can have a profound effect on the macroevolutionary process itself, facilitating sympatric speciation in the population. Here, as in the Baldwin effect (Baldwin, 1896; Hinton & Nowlan, 1987), the autarchy of blind evolution can be swayed by the adaptive powers of the individual. These phenomena challenge the usual hierarchical picture of adaptive processes, in which evolution shapes behavior without behavior affecting evolution, and suggest a more complex, realistic, and balanced view of the relations among evolution, learning, and behavior.

Parental imprinting and other forms of mate choice are mechanisms of adaptive behavior. They have evolved in so many species because adapting to the ever-changing composition of one's own species is just as important and challenging as adapting to the rest of the environment. If we want to understand *all* the mechanisms of adaptive behavior in animals, we have to study those designed for reproduction as well as survival. It is a happy coincidence (or perhaps a deeper truth) that in studying mechanisms for adaptive reproduction, we may come on some that actually increase the power of macroevolution itself and that might, in turn, be used to increase the efficiency of our artificial evolutionary techniques applied to design optimization and other problems. Thus, whether for scientific understanding or engineering applications, it is important to study the mechanisms underlying all domains of adaptive behavior in autonomous agents, including both survival and reproduction.

Acknowledgments

Geoffrey Miller has been supported by a National Science Foundation (NSF) postdoctoral research grant INT-9203229, by an NSF graduate fellowship, and by NSF grant BNS90-21684 to Roger Shepard.

For comments, support, advice, or inspiration relevant to this work, we authors are indebted to George Barlow, Helena Cronin, Phil Husbands, Andrew Pomiankowski, and John Maynard Smith.

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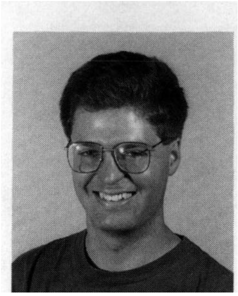

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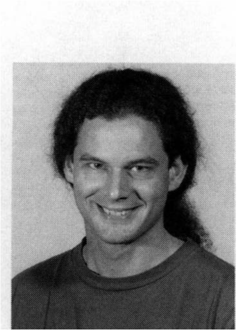

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