



Mother Nature

*A History of
Mothers, Infants, and
Natural Selection*

Sarah Blaffer Hrdy

Also by Sarah Blaffer Hrdy:

The Woman That Never Evolved

The Langurs of Abu: Female and Male Strategies of Reproduction

The Black-man of Zinacantan: A Central American Legend

Co-editor with Glenn Hausfater:

Infanticide: Comparative and Evolutionary Perspectives

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*For Dan,
the wisest choice this female ever made*

Most surprising were all the ways that mothers influence their offspring's development through both genetic (including female choice) and nongenetic effects. The updated image of old Flo, for example, allows us a glimpse into the significance of such "maternal effects." Fifi, Flo's daughter, entered the world advantaged by her mother's rank, a maternal effect that pointed to ever more subtle ways—beyond genetically inherited attributes and succor—through which mothers influence the fates of their offspring. By the end of the twentieth century, the spotlight shifted so as to begin to illuminate in rigorous and controlled studies how organisms develop in specific contexts. Development would turn out to be the critical missing link in evolutionary thinking.

Underlying Mysteries of Development

To me the Development Theory [Spencer's term for evolution] and all other explanations of processes by which things came to be produce a feeble impression compared with the mystery that lies under the processes.

—George Eliot, letter to a friend on reading Darwin's *Origin*, 1859

I suspect that many sophisticated biologists remain skeptical about selection . . . because of mysteries such as how ontogenies work.

—Richard Alexander, 1997

One reason for our fascination with Princess Diana is her Cinderella-like life story: unknown ingenue transformed into a future queen. Beekeepers routinely make such fairy tales come true just by arranging for the eggs or young larvae (less than three days old) to be fed a substance called "royal jelly."

As an egg or larva, females are totipotent, able to develop into several different forms. In the honeybee world, in which "you are what you eat," a female's lot in life—what one might think of as her class (strictly speaking, her "caste")—is determined not by her genes but by what her nurses *feed her* and by the reproductive oppression of dominant individuals. Ditto for what we might call her gender—whether or not she becomes an imperious mother or servile spinster sister.

At oviposition, the egg that will be queen is placed in a special compartment. She spends her privileged larvahood being fed a chemical concoction—royal jelly—prepared in the salivary glands of her nurses. The body of the immature, specially fed individual matures so as to differ from the ordinary worker in fifty-three different morphological and behavioral respects. Instead of becoming a sterile worker who will never produce an offspring, she blossoms into a fecund queen who will produce several million of them.¹ Two females with virtually identical *genotypes* (genetic composition at con-

ception) look forward to two utterly different destinies. Intervening events resulting in these different outcomes constitute the underlying mysteries.

The Importance of Development

Even prior to merging of sperm with egg, even before there is anything that could be thought of as a conceptus, an embryo, or an “organism,” future possibilities are being shaped by the ambient surroundings of the germ cells. In mammals, these surroundings are influenced by the mother’s internal state, by nutrients in the protoplasm a mother adds to her eggs, or, as in the case of honeybees, by nutrients provided by other members of the colony.

The mysterious development of individuals, or ontogeny, includes all those complex and opportunistic emergent processes that affect how each genotype develops into the *phenotype*, the tangible properties of the organism that are influenced but never entirely determined by genes.² Phenotype is one of those awkward umbrella terms that began narrow, then opened up through time to cover a larger area. Today the term is still used in the original way, to describe specific ways that genes are expressed (as in a particular eye color or blood type); but phenotype is also used to refer to an entire organism, or its behavior.

The important point here is that all anyone ever sees, touches, or directly experiences is phenotypes, never genes. It is phenotypes that interface with the world and interact with others in it. Only phenotypes are directly exposed to natural selection. This is why, evolutionarily speaking, and especially for those like me who study behavior, phenotypes are what matters.

Phenotypes are produced by interactions between genes and other environmental or parental influences. They can be affected by all kinds of variables—how much cytoplasm the mother delivers in the egg, what other chemicals she adds, what time of year it is, what the mother is eating at the time, diseases she might have, even her own recent social history. This is why sociobiologist Mary Jane West-Eberhard can state so adamantly: “Nothing is genetically determined in the sense of determined by genes alone. No gene is expressed except under particular circumstances. . . . It’s a kind of biological illiteracy to talk about a gene *for* anything other than a particular protein molecule.”³

West-Eberhard is not saying that genes don’t matter but rather that their powers are inseparable from context, including both external context and

the developmental context, since genes act by influencing a responsive structure that is already there. This is true at every level, from immune-system defenses at the cellular level to character at the personality level. It is as absurd to talk about behavior being “genetically determined” as it is to claim that genes have nothing to do with behavior.

It is profoundly incorrect to equate “genetic” with “biological,” a term that covers far more than just genetic processes. It is also incorrect to treat nature and nurture as separable entities, as in saying “The genes interact with the environment,” or “Nurture does not matter.” This is why it is unfortunate to hear the label “biological mother” applied to a woman who has given birth to a child and given it up for adoption, or, worse, just provided the donor egg. Such a woman is more nearly the *genetic* or *gestational* mother. By contrast to a genetic donor, the *biological* mother nourishes, nurtures, and provides the environment in which the infant develops both physically and psychologically.⁴

It is clear that genes are not puppeteers directing behavior. A range of nongenetic factors, such as mother’s physical condition or social status, the season when she conceived, her own diet or the one she provided her baby, the presence or absence of father—all contribute to individualization. Parental effects encompass all the nongenetically transmitted attributes that pass from parent to offspring. Practically speaking, the mediators of such effects are often mothers. Not hereditary in any genetic sense, maternal effects can nevertheless influence the speed and course of evolutionary change, trends that sooner or later lead to changes in gene frequency—the stuff of evolution.

The dynamics of genetic and maternal effects are relatively better understood in the mother-centered worlds of hymenopteran social insects—honeybees, wasps, and ants—than they are in other animals. A finite number of chemical signals chart an individual’s life course, thus permitting scientists to carry out rigorously controlled experiments showing how a specific treatment (such as feeding royal jelly) plays out during development. One of the ironies of the charge “genetic determinism” so often leveled at sociobiologists is that so many of its earliest practitioners—Edward O. Wilson, Mary Jane West-Eberhard, William Hamilton, and Richard Alexander—were also entomologists. They were acutely aware that genetics does not equal biology. They didn’t call the new field sociogenetics; they called it sociobiology—for a reason.

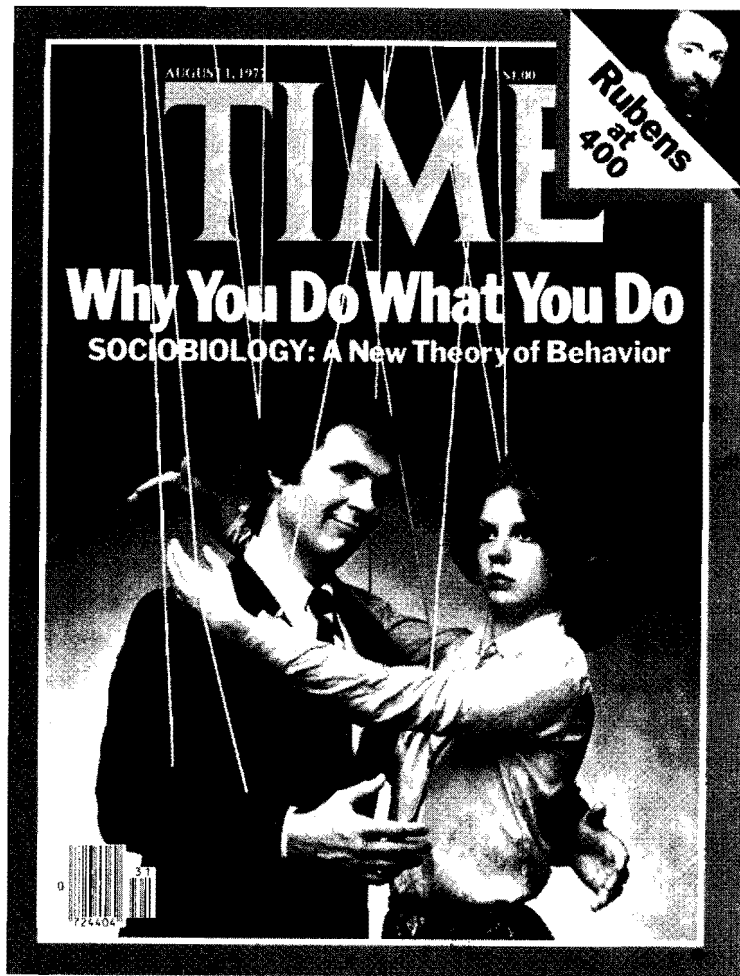


Fig. 3.1 Genetically orchestrated couple on strings dance woodenly across the August 1, 1977, cover of *Time*. The magazine promises to tell how “a new theory would explain” just “Why You Do What You Do.” Images of genes controlling people like puppets are more often invoked by critics of sociobiology than its practitioners. (© 1977 Time Inc.; reprinted by permission)

Mother-Centered Worlds

Nineteenth-century evolutionists knew that traits were inherited, but they did not know of the existence of genes or understand how they worked. They lacked a way of conceptualizing the complicated relationship between inher-

ited traits and alternative outcomes, or phenotypes. As late as the 1950s most animal behaviorists still took it for granted that relatively brainless, cultureless creatures like honeybees were born to function instinctively in a narrowly specified, or species-typical, way. Workers were predestined from birth to serve the queen and maintain the efficiency of the hive.

In 1894, Darwin’s associate Thomas Henry Huxley could write confidently—in what he considered a progressive statement—that the “vast and fundamental difference between bee society and human society” was that bees “are each organically predestined to the performance of one particular class of functions only,” while among men “there is no such predestination.” Among men “it cannot be said that one is fitted by his organization to be an agricultural laborer and nothing else, and another to be a landowner and nothing else.”⁵

No modern sociobiologist would disagree with Huxley’s assessment that each human individual is born with variable potential. But most would emphatically disagree with Huxley’s assumption that the lot of a hymenopteran insect was quite so narrowly predestined. Far from strict destiny—a direct equation of genotype with phenotype—a honeybee’s gender is merely a potential. Even in an organism born so mindless as a bee, a creature who learns remarkably little in the course of her life, a female has the potential to become *either* a worker *or* a queen, depending on the type of nurture she receives. Even whether or not a worker remains sterile or takes a stab at laying eggs turns out to be negotiable.

Gender, Relatedness, and Caste

The reproductive subservience of worker castes is not quite so voluntary as believed. The honeybee queen manufactures a special “queen substance” in her mandibular gland that broadcasts an imperious olfactory message informing workers of the hive: “Develop your ovaries and you’re dead!” The hormonal signals (or *pheromones*) that the queen uses to broadcast this message are derived from ancient hormones emitted by one insect to threaten another in the course of female-female competition.⁶ In response to peremptory pheromonal signals passed bee-to-bee during food exchange, the workers’ ovaries shut down. Yet occasionally—in spite of all this propaganda—a worker may attempt to lay eggs. But her efforts are usually in vain. Her eggs will most likely be cannibalized by other females who detect them.

Ovarian despotism by dominant females has been especially well studied in the genus *Polistes*. These hornet-like wasps range throughout North America and down to Central America. They sting like fire. Fortunately, though, many species are easy to spot due to conspicuous black, yellow, and burnt sienna body bands. If it is summer outside, paper wasps are probably, at this moment, busily constructing parchment-like nests of chewed wood pulp in the eaves of your building.

In an ingeniously simple manipulation, Mary Jane West-Eberhard—who for many years has studied the tropical paper wasps near her homes in Colombia and Costa Rica—tethered a reproductive female some distance from where her eggs had been laid by tying a slender nylon thread around the wasp's waist. As soon as this dominant female was prevented from aggressively defending exclusive access to the nest, the previously suppressed ovaries of her daughters revved up and they began laying eggs.⁷

Seemingly utopian, the paper wasps' society is more nearly an ovarian police state. This does not necessarily mean there is no future to unauthorized fecundity. Some Argentinean ants give destiny a helpful nudge by assassinating the dominant female, usurping her breeding prerogatives for themselves.⁸ More often, however, the better part of valor for a worker in these mother-centered, mother-dominated societies turns out to be helping their foundress—or, once the colony gets going, their sister—to rear her offspring.

Even in honeybees, which, most would agree, do approximate buzzing automatons, genes do not determine outcome in life decisions as major as whether to become a mother. Rather, genes set limits on a range of developmental outcomes, which are very few compared with the situation in humans, where the range of outcomes is enormous—albeit still not infinite.⁹

Genes, with all their limitations, nevertheless play a very special role in the puzzle posed by highly cooperative breeding colonies of social insects. If all living things strive to reproduce, as Darwin theorized, how could one explain the dedication of the altruistic worker bees who will never reproduce and transmit genes to future generations? This challenge to Darwinian theory yielded to an ingenious solution proposed in 1963 by British geneticist William Hamilton. This reserved and self-effacing young scientist came up with a bold idea—selection at the level of kin—to explain the altruism of the queen's sterile attendants.¹⁰

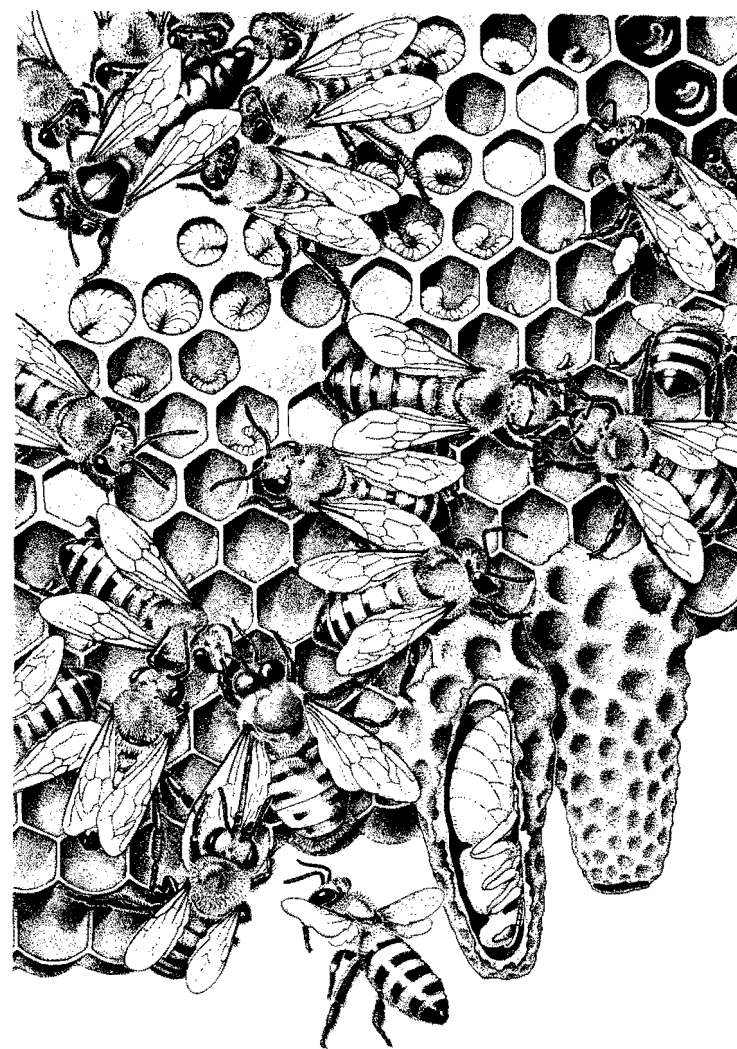


Fig. 3.2 Eusocial insects live in colonies with overlapping generations that include sterile, nonreproductive castes. Here a honeybee queen is surrounded by her worker-bee daughters who forage for pollen and then regurgitate it as nectar into the mouths of other workers. These workers add special enzymes to produce honey before storing it in the hexagonal wax cells of the honeycomb. The queen lays up to 2,000 eggs a day, tended by these workers.¹¹ Only one in tens of thousands of females ever becomes a mother herself. *Lower left:* One of the queen's daughters drags away a drone by his wings. Males in this world are the odd men out, disadvantaged because they are more distantly related. If entomologists got their degrees in humanities departments, perhaps we would have libraries full of dissertations analyzing "gender, relatedness, and caste"—honeybee style. (Reprinted by permission of the publisher from *Insect Societies* by E. O. Wilson [illustration by Sarah Landry], Harvard University Press, Copyright © 1971 by the President and Fellows of Harvard College)

Hamilton's Rule

The civic-mindedness of sterile workers earns honeybees the utopian designation *eusocial* (or, “perfectly social”), which applies to any society with overlapping generations devoted to the cooperative care of immatures and characterized by specialized reproductive and nonreproductive castes. Although young are produced in great quantity, it is the quality of the care that enables so many to survive. Busy workers spend the first three weeks of their short lives in the hive, tending their sister's young, and their next (and final) three weeks foraging for nectar in the riskier world outside.

To explain this world, Hamilton drew on his knowledge of the special reproductive attributes of social insects. He proposed that hymenopteran social insects so often put the colony's interests ahead of their own because of an especially close degree of genetic relatedness between the workers and the queen. This comes about because of an odd biological circumstance by which males have just one set of chromosomes (haploid), while females have two sets (diploid), so that organisms such as wasps engage in “haplodiploid” reproduction. In haplodiploid organisms, two sisters with the same father will share more genes in common than a mother shares with her own offspring.¹²

Primitive as they may seem, even insects have hidden zones of ovarian decision-making. Once a honeybee queen or a reproductive wasp mates, she stores the sperm in a special pouch called a *spermatheca*. When she lays an egg, she has the option of opening a valve, permitting sperm to fertilize it as it passes through her reproductive tract. A fertilized egg with two sets of chromosomes (diploid) develops into a daughter. As with most sexually reproducing animals, the resulting daughter receives half of her chromosomes from her mother, the other half from the male with whom the queen mated. But if the queen withholds sperm, something unusual happens. The unfertilized egg develops anyway, but it develops into a haploid individual with only one set of chromosomes, derived entirely from her. Haploid eggs always develop into sons. Since any male the queen mates with is haploid, this creates a peculiar skew for her female offspring, such that sisters are especially closely related. This is why the genetic payoff for a worker investing in the queen's offspring is greater than if she produced her own. Male honeybees don't have this same especially close relationship to the queen's offspring and also don't meet this same test of citizenship.

These drones, or “winged sperm dispensers” (as Ed Wilson terms them),

live only long enough to mate and then die. After reaching adulthood, they spend a few days in the nest before taking off for their big (also final) moment on the mating flight. Nonmating males are either driven out of the colony or killed.¹³

Instead of focusing on the sterile worker's genetic representation in the next generation—which would be zero—Hamilton expanded the concept of an individual's lifetime reproductive success (or *fitness*) to include the *inclusive fitness* of the individual. By inclusive fitness Hamilton meant the effect that the female worker's behavior has on her own fitness *plus* the effects her behavior has on the fitness of close kin who share genes by common descent. Using this principle, Hamilton derived simple mathematical expressions predicting that altruism should evolve whenever the cost to the giver (which he designated C) was less than the fitness benefits (B) obtained by helping another individual who was related by r , a term designating the proportion of genes these two individuals shared by common descent.¹⁴

Hamilton's deceptively simple-looking equation $C < Br$ underlies the evolution of helping behavior in all social creatures. The rule together with the general theory behind kin selection were almost immediately confirmed by West-Eberhard for wasps,¹⁵ and soon after for many other animals.¹⁶ At an ultimate level, kin selection explains the universal human pattern of favoring kin. In humans different beliefs and customs underlie these patterns, but the outcome is everywhere the same: kin preferred to nonkin.¹⁷ Indeed, as we will see, many unexpected features of maternal behavior can be understood as special cases of Hamilton's rule.

No gene or set of genes, or even any one mechanism influencing people to favor kin, has been identified. We do not know even a fraction of the ways that kin selection works. Yet wherever biologists or anthropologists have looked, animals, including people, behave *as if* there were such genes. One way or another (and, as I say, nobody understands how) all social creatures have through evolutionary time—probably in different ways—internalized Hamilton's rule.¹⁸ In humans we can only assume that our powerful predisposition to prefer our own kin derives from very ancient emotional and cognitive systems, such as learning to recognize people familiar from a very early age and having a lower threshold for altruism in our behavior toward them. This is the simplest explanation for our similarities with other social creatures in this respect.

As Hamilton expressed it:

[In theory] a gene causing altruistic behaviour towards brothers or sisters will be selected only if the behaviour and the circumstances are generally such that the gain is more than twice the loss. . . . To put the matter more vividly, an animal acting on this principle would sacrifice its life if it could thereby save more than two brothers, but not for less.¹⁹

And this is where the matter has stood for many years, the emphasis in “kin selection” on the close relatedness of the actors.

However, not all social insects with remarkably cooperative breeding systems have this kind of special haplodiploid reproduction. (Termites, for example, do not.) For this reason, attention has begun to shift to the other components of Hamilton’s initial equation: the ratio of costs and benefits to actors. The honeybee queen, recall, grows up to be a specialist in egg-laying. She is a super-mother in a class by herself, a female of enlarged ovaries, able to lay an egg a minute, day and night, for up to five years. Her worker sister, on the other hand, even if she manages to produce some eggs, has severely limited prospects of rearing them. How much, then, does a sterile worker actually give up by altruistically helping her mother or her sister reproduce, accepting a fractional interest in millions of eggs instead of laying a few ill-fated ones herself? What are the costs in relation to benefits, given the females’ degree of relatedness?

By themselves, the peculiarities of haplodiploid genetic systems do not fully explain why ants, wasps, bees, termites, and other eusocial insects must be counted among nature’s longest-lived and most fecund success stories. Something else is needed to explain 140 million years of eusocial prosperity. We need to keep in mind Mother Nature’s cardinal rule for mothers: It’s not enough to produce offspring; to succeed through evolutionary time mothers must produce offspring who will survive and prosper. In short, we need to consider the importance of what I think of as “the daycare factor.”

In an unrivaled reproductive success story, expeditions of leaf-cutting and harvester ants blaze trails across the forest floor, while battalions of army ants terrorize mammals in their path. Bees and wasps dot trees with their nests,

and termites infest rotting wood. One-third of the animal biomass of the Amazonian rain forest teems, climbs, and swarms with billions upon billions of these social insects.²⁰

The secret to their success is, quite simply, the most dedicated and efficient daycare in the biosphere. So what if some army-ant queens can lay up to two million eggs? A woman starts out her life with more than three times that many egg cells. It’s not the insect queen’s fecundity that is so special, it’s her success rate translating eggs into adult survivors. What makes social insects so amazing is the dedicated assistance of all those allomothers. Even if the mother dies, so long as the colony persists, her progeny will be cared for.²¹ It is a mother-centered world geared toward one aim: the survival of progeny.

Controlling Mothers?

She’s a real Queen Bee! We use the term, often with a tinge of disapprobation, to describe a despot, a figure in charge. It’s one of those metaphors that on closer inspection is more apt than people realize. But even without a queendom, some solitary wasp mothers who do not found large breeding cooperatives—like the fig wasp mother who breeds alone—nevertheless manage to exercise remarkable control over their posterity. Their power derives from their ability to predetermine the sex of each offspring.

William Hamilton showed how a solitary mother fig wasp ruthlessly manipulates her progeny in ways that suit her long-term reproductive interests. As the female lays each egg, she either fertilizes it or not, thus determining the exact configuration of daughters and sons, which she can translate into the greatest number of grand-offspring. Out of a batch of 257 eggs, one mother produced 235 daughters and just 22 sons. To explain this wildly female-biased sex ratio, Hamilton devised a theory based on local competition for mates, generally referred to as “local mate competition.”

Local mate competition? What could a mother’s production of sons versus daughters possibly have to do with competition to breed? Normally not much, not in outbred creatures like ourselves who avoid mating with full siblings. But in the incestuous world of the fig wasp, the number of daughters for every son matters a great deal. The wasp mother’s brood will be born, and breed, right there within the fleshy pink confines of the fig. “Local mate competition” is an understatement. Brothers born just a hairsbreadth away from one another wait outside the nursery until the sisters hatch, then use their



Fig. 3.4 William D. Hamilton describes the incestuous microcosm inside a fig, while evolutionary theorist Robert Trivers looks on. Hamilton's 1967 article "Extraordinary Sex Ratios" explained why the mother fig wasp produces mostly daughters. I used to attend their seminars, bringing my infant daughter with me. Since she was asleep in a canvas carry-all, my hands were free to take this photograph. (Sarah Blaffer Hrdy/Anthro-Photo)

ton's theory of local mate competition in every detail, the jewel in this crown, was an unlikely candidate in all but name. *Nasonia vitripennis* is a tiny parasitoid wasp, smaller than a fruit fly, with the unsavory habit of laying eggs on the pupae of blowflies laid under carcasses and in birds' nests. This parasite upon a parasite is commonly known as the jewel wasp.

The parasitic jewel wasp, turns out to be, in the words of biologist John Werren, "a consummate artist at controlling the sex of [her] offspring." Similar to Hamilton's fig wasps, jewel wasp mothers locate a blowfly pupa and lay eggs, most of which will hatch as daughters, with just enough sons—perhaps 15 percent of the eggs—to inseminate them. Unattractive as their housing requirements happen to be, space is in short supply. What happens, John Werren wondered, if the mother arrives at her host, injects her stinger (which is also a sensory organ) into the mush, only to detect chemically that another mother got there first and had already deposited *her* eggs? At that point, this family-planner par excellence inserts only a single, unfertilized (and therefore male) egg. Her son will hatch into a world full of opportunities: he will join the fray with sons of the first female, competing to copulate with her daughters.

Yet even a mother so much in control as the jewel wasp rarely has the last word. Werren discovered a "parasite" upon this calculating parasite. About 10 percent of jewel wasps carry a particular virus-like gene known as "the paternal sex ratio element." If the male the mother mates with carries it, that male transmits it to her in his sperm. This parasitic gene destroys the paternal chromosomes in all the eggs that she fertilizes, converting all diploid eggs into haploid ones. The fertilized eggs that normally would have developed into daughters become sons, the only sex host capable of transmitting the parasitic gene. This parasite upon a parasite upon a parasite could theoretically cause jewel wasps to become extinct by artificially producing an all-male population.

But Werren, with the geneticist's optimism that every dilemma is only a mutation away from some sort of solution, chose to look on the bright side. Instead of predicting extinction, he quotes Jonathan Swift:

*So, Nat'ralists observe, a Flea
Hath smaller Fleas that on him prey;
And these have smaller fleas to bite 'em
And so proceed ad infinitum.²⁴*

By the 1970s, then, entomologists exploring cooperative infant rearing, maternal manipulation of sex ratios, and suppression of ovulation were not just discovering new dimensions to being female; they were uncovering new dimensions to *individuality* that had to do with development. Hamilton's rule provided sociobiologists with a universal truth: it applied to all social organisms, *all other things being equal*. But when are all other things ever equal? Especially in a formula that has built into it functions like "cost to an organism" and "benefit." It's impossible to consider these without reference to the environment in which organisms develop, the age and condition of the individual, and constraints imposed by others in that environment.

Maternal Effects

For species such as primates, the mother *is* the environment, or at least the most important feature in it during the most perilous phase in any individual's existence. Her luck, plus how well she copes with her world—its

scarcities, its predators, its pathogens, along with her conspecifics in it—are what determine whether or not a fertilization ever counts.

What mothers are and do can facilitate or impede adaptation to new conditions, impart to immatures a mother's own immunological defenses (through lactation) or otherwise give youngsters a boost. These head-start programs can begin even before fertilization (see Plate 1).

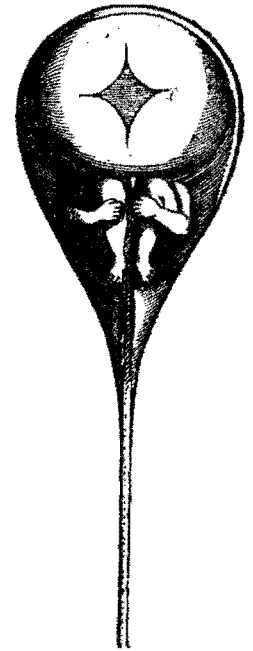
During the late seventeenth century, scientists thought they saw a miniature man, a little "homunculus," through their microscopes, folded up inside a human sperm, waiting to be deposited inside the womb. Even after 1827, when embryologist Karl Ernst von Baer provided a more accurate description of the mammalian egg and convinced his colleagues that miniature humans were not planted ready-made into the uteruses of women,²⁵ it continued to be assumed for another century that males alone directed the course of evolution. Even though mothers contributed egg cells, they were viewed as passive vessels, awaiting the life force conveyed by males.

But this, too, was not quite right. Rather than being penetrated by a sperm, the egg (or oocyte) more nearly engulfs it, quite possibly selecting which sperm to accept, and producing specific chemicals that are necessary for fertilization to take place. The sperm cell is almost pure nucleus; the oocyte contains several ingredients—nucleus and cytoplasm. Once the sperm is inside the egg, maternally transmitted instructions go to work. Nutrients stockpiled prior to fertilization supply the needs of the developing embryo. In particular, the mother's oocyte is derived from cells that, even prior to fertilization, have begun dividing. Prior to any contact with the sperm, the maternal germ cell has divided four times, into sixteen cells. One of these continues on as the oocyte. The others become "nurse cells," which manufacture nutrients and other materials that will be transmitted through the cytoplasm.²⁶

This means that early embryonic development is under maternal control before the father's genes, carried by the sperm, are even activated. At the outset, the egg's acceptance of a sperm launches maternal effects. Protoplasm from the mother sets up the embryo for development, prelude to many possible maternal effects.

One of the strangest and least anticipated maternal effects ever described has to do with just such special ingredients transmitted by the mother to the cytoplasm in her eggs. It is a case that belies all stereotypical expectations about maternal virtue, defying the conventional expectation that a

Fig. 3.5 Drawing of "homunculus" from Nicolas Hartsoecker's *Essay de Dioptrique*, 1694.



"madonna" ought to make a more suitable mother than a "whore." In this instance, it is the *femmes fatales* who make the best mothers.

Imagine flashing lights blinking on a sultry night. But these lights are not inviting summer vacationers to visit discos. The strobe effect emanates from luminous, phosphorescent organs on the abdomens of *Photuris* fireflies. These female fireflies emit chemically produced flashes of light that mimic the mate-attracting signal of another species, a type of firefly belonging to the related genus *Photinus*, in which females really did evolve to signal readiness to mate by flashing and males evolved through sexual selection to seek them out when they did. But when an eager *Photinus* suitor shows up, the alluring *Photuris* female eats him instead of mating with him.

The *Photuris*-mother-to-be gets more than a meal out of this male. She also gets his armor, since her victim has the unusual capacity to manufacture defensive steroids that make him unpalatable to birds and predatory spiders. The mother promptly passes this chemical protection on to the eggs she is laying, endowing them with her chemical booty.²⁷

Such cases are the stock-in-trade of those sociobiologists like Mary Jane West-Eberhard who focus on development. To her, individualization begins as a maternal effect. "An animal egg or a plant seed is already a highly organized and active phenotype before it is fertilized." She entreats us to consider the beginning of a frog's life. Hours after fertilization, with the fast-dividing blastula (the early development phase of an animal) already 4,000 cells strong, none of the embryo's own genes have been activated. The only instructions to be had are from hormones and proteins circulating in the

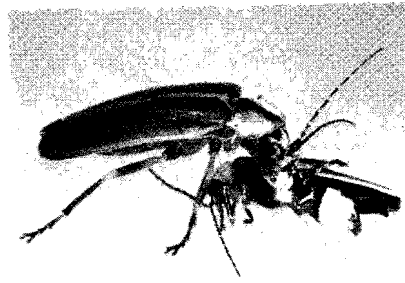


Fig. 3.6 Female *Photuris* fireflies mimic the sexually selected mating signal of another species, *Photinus*. When unsuspecting *Photinus* males arrive to mate, the deceptive females eat them, ingesting their defensive chemicals, which are passed along to their offspring. Thus, through the trickery of their mothers, *Photuris* offspring enjoy an increased chance of surviving to adulthood.

(Courtesy of Thomas Eisner)

cytoplasm. Far from genetically determined, initial development of this new individual, with its “hand-me-down phenotype,” is very much influenced by maternal condition, her nutritional status or life history. This is what West-Eberhard means when she scoffs that “The bare genes are among the most impotent and useless materials imaginable.” Thus the phenotype of the early embryo is determined by the mother alone. This represents a maternal effect undreamed of before the closing years of the twentieth century.²⁸

West-Eberhard has been foremost among those working to integrate behavioral plasticity in both sexes into evolutionary theory. What fascinates this wasp specialist is the extent to which genetically similar individuals can be shunted into different pathways of development according to conditions encountered early in life. The identical genotype (or at least genotypes that are very similar, as in full siblings) could develop into an organism that looks or behaves very differently (that is, exhibits a different phenotype).²⁹

The phenomenon of environmentally cued alternative phenotypes within the same population is known as *polyphenism* (i.e., same genotype produces more than one phenotype). Long overlooked, polyphenism, the outcome of so many underlying mysteries, is assuming greater importance in the thinking of geneticists. Anyone tempted by cascading research that identifies genes “for” particular traits would do well to keep these cases in mind, as reminders of how much context still matters.

Catkins or Twigs

The reason all the best examples of polyphenism derive from plants and insects rather than vertebrates is purely practical. To obtain unambiguous experimental results requires the experimenter to rear identical individuals

under different conditions. Distinctive life-forms (or morphs) found in easy-to-manipulate insects, together with their short lifespans, means that study subjects can grow up, breed, die, and yield definitive results quickly—before funding to study them runs out.

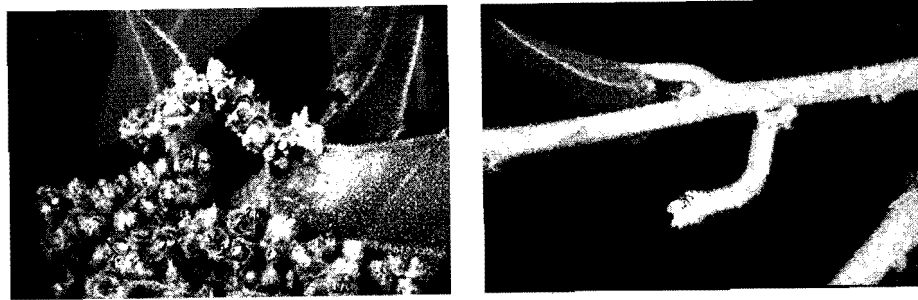
My favorite example comes from caterpillars belonging to a species of geometrid moths (*Nemoria arizonaria*) that breed in oak woodlands across the American Southwest. Entomologist Erick Greene used these caterpillars to demonstrate how different diets early in life produce utterly different morphs—organisms as different as two species. In the process, Greene showed how peculiar contingencies of a mother’s existence—whether she gave birth early in the season or later—factor into the shapes her offspring must assume to survive.

In the case of the geometrid moths, mothers hatch two broods of caterpillars each year. In nature, spring broods feed on the protein-rich pollen of the oak’s drooping flowers, called catkins. Long after these kittens’ tails (their name derives from the Dutch diminutive, *katte*, precisely because of this resemblance) have dropped from the trees, the second (summer) brood of caterpillars hatches. Since the catkins are gone, all that is left for summer caterpillars are tough, mature oak leaves, laden with tannins, which are poisonous compounds produced by oaks to discourage nibblers. But in a world where caterpillars are what they eat, these tough leaves are just the ticket.

Whereas pollen-eating grubs metamorphose into knobby, wrinkled caterpillars that resemble oak stamens, looking to all the world (especially to hungry birds that prey on insect larvae but not plants) like drooping catkins, later-born morphs are gray-green, less knobby, and utterly twiglike, blending in with their leafy dinner and once again fooling predators. High levels of tannin from the leaves (or something associated with them) trigger the development of this twiglike morph.

Greene’s elegant experiments showed that the pathway taken by the genetically coded developmental program is triggered by what the caterpillar eats in the first three days. If early broods eat fibery leaves instead of pollen, they, too, come to resemble twigs.³⁰

The nutritionally superior catkin diet permits spring broods to attain a larger size by the time they pupate, to mature faster, survive better, and (once they become moths) to be more fecund breeders. Despite the disadvantages of being born late, caterpillar lines that failed to produce summer broods miss out on the opportunity to breed twice in the same year.



Figs. 3.7a and b When Erick Greene experimentally fed full sibs of the caterpillar *Nemoria arizonaria* different diets, two different morphs developed. Spring and summer broods look the same when they first hatch, but subsequently the early-born (spring) broods feed on oak catkins and grow up to look like drooping flowers. Later-born (summer) broods subsist on leaves and develop into alternative morphs camouflaged as twigs. If summer broods were artificially fed out-of-season catkin meals, they would stand out like solitary kitten's tails within an inland sea of twigs and leaves, easily spotted by predators. (Reprinted with permission from *Science* 243:644. © 1989 American Association for the Advancement of Science)

Alternative Outcomes of Development

Genetically identical individuals can grow up to be very different—that is, to have very different phenotypes—depending on circumstances encountered early in development. These flexible phenotypes result in different “morphs” or types of individuals. Simply put, in varied and unpredictable worlds there will be more than one way to survive and reproduce. Through the course of development, individuals adopt alternative strategies, manifested either in their morphology and physical appearance or in their behavior. Resulting phenotypes depend on circumstances, on which genes or receptors are switched on, which cellular and bodily responses triggered. Alternate phenotypes, or ways of being, are coded right into the genetic constitution (or genome) of the same individual.

Polyphenism, with its multiple developmental courses, is too useful a concept to confine to “simple” creatures like wasps and caterpillars. Increasingly, biologists are aware that mammals—including primates like ourselves—can develop along different pathways, even assume different forms or exhibit quite different behavioral profiles, depending on what developmental track they find themselves on. However, the underlying mysteries in large-bodied, socially complex, and long-lived organisms are far harder to pin down exper-

imentally, and none of the cases could be so well documented as in the honeybees and caterpillars. Consider the “Peter Pan” orangutans.

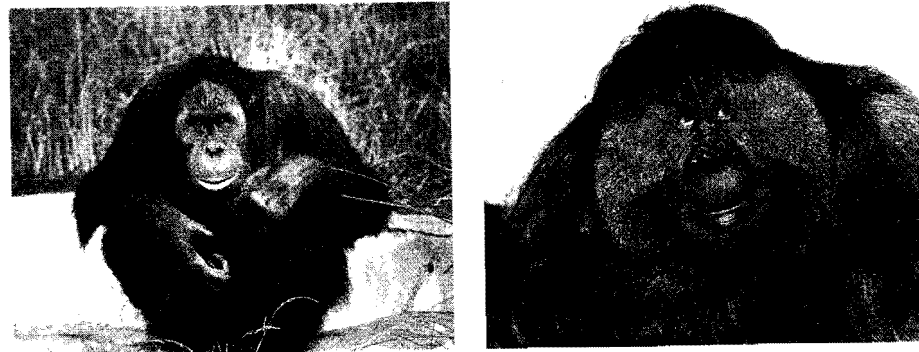
Researchers engaged in long-term studies of orangutans in the wild have long been puzzled by the curious case of males who never seem to grow up. The “Peter Pans” are so different from full adult males that the legendary naturalist Alfred Russell Wallace (the codiscoverer of Darwin’s theory of natural selection), on encountering one, assumed he belonged to a different species. Various biologists since have made the same mistake.

The two orangutan body types (or morphs) are characterized by utterly different patterns of growth and reproduction; year after year, the same males get classified as adolescents—in some cases, for as long as twenty years. But if, one day, the dominant male disappears, the Peter Pan male undergoes a transformation: within months his face fills out, his hair grows, and he accumulates bulk. Abandoning his low profile for the life of a bully, it is Peter Pan’s turn to patrol the forest like a quarrelsome troubadour in quest of a maiden, uttering deep roars and fighting any other adult male he meets.³¹

Primatologists Peter Rodman and Biruté Galdikas, who study orangs in the forests of Borneo, have described the low-cost, low-benefit mating strategy pursued by undersized, adolescent-looking males who skulk about females and copulate with them even though they are not sexually receptive. (Galdikas labels this the “sneak/rape” strategy, the only thing approaching rape in a primate other than humans.) Such males are seemingly unselective, attempting to copulate as often as possible, even at times of her cycle when the female is unlikely to conceive.

By contrast, a full adult male is more discriminating and concentrates on ovulating females. Such a male fiercely defends access to one, and fights to the death to drive rival males from her vicinity, thus maximizing his chance of being the father of her next offspring. This “combat/consort” strategy is far more costly than the sneaker’s tactics in terms of risk to the male from combat. Furthermore, the adult male’s discriminating standards mean that big males copulate only rarely (ovulating female orangs being an exceedingly scarce commodity in these highly dispersed and slow-breeding apes). Nevertheless, such copulations as the consorting big males do obtain are more likely to culminate in conception.

West-Eberhard was so impressed by the evolutionary possibilities of this kind of variation—far more common than generally realized—that she sug-



Figs. 3. 8a and b The orang on the left is a “developmentally arrested” Peter Pan male. On the right is a full adult male with beard and full cheek flanges. He has much higher testosterone levels, and exudes a musky odor. Developmentally arrested males maintain a low profile and attract less aggression from dominant males. But as soon as the locally dominant male is removed, the Peter Pan male grows up, develops protruding cheek flanges, and emits long calls, turning into the very model of a Darwinian male who (as described in the *Descent of Man*) “expends much force in fierce contests with his rivals, in wandering about in search of the female, in exerting his voice, pouring out odoriferous secretions, etc.” (Photos by Jessie Cohen, National Zoological Park, © Smithsonian Institution)

gested organisms may use multiple morphologies or lifestyles (say, eating one food rather than another) to “experiment” with new niches. If the trial run proves successful, and animals pursuing this new lifestyle survive and reproduce better, then new evolutionary opportunities are opened up. For example, a population of caterpillars could conceivably evolve to specialize in eating leaves high in tannins all the time. Or (to really engage in science fiction), if forest fires continued to burn in Indonesia and food was chronically short, selection might favor a Peter Pan morph who was inclined to never grow big.

Multiple phenotypes provide natural selection an opportunity to either favor or penalize genetic combinations that predispose animals to live some novel way. Such phenotypic flexibility means that evolution and speciation can occur at a faster pace than would otherwise be possible.³²

Memes and Other Special Maternal Effects

In terms of evolution, some of the most stunning maternal effects are produced by information about the world communicated by a mother to her infant. Such information can be transmitted chemically (experiments with rats show that food choices later in life are influenced by molecules in

mother’s milk) or through cultural concepts, which is possible only in species endowed with language and symbolic reasoning. Though there may have been other hominids so endowed in the past, *Homo sapiens* is the unique possessor of these capacities today.³³

The hand that rocks the cradle rarely controls the world. But the voice that sings the lullabies and barks cautionary messages in the first years of life provides critical information about the social niche into which the child has been born. Such experiences can have a lasting effect upon his mental and emotional outlook. Through her example and direct teaching, a mother shapes critical assumptions about how the world works, what there is to eat, who there is to be afraid of, who is likely to be well-disposed, and so forth—myriad units of culturally transmitted information, or “memes.”³⁴

Human self-images and beliefs are not frozen and continue to change through life as individuals (active agents in their own right) encounter new social opportunities and constraints. But the fact that immature humans are so impressionable has evolutionary consequences out of proportion to the brief time period when immatures are intimately exposed to their mothers and to her immediate circumstances, or “local history.”

A distinguished roster of evolutionists (including Ernst Mayr, John Emlen, George Williams, Edward O. Wilson, and Richard Dawkins) have all commented on the extraordinary gullibility of our species, especially when we are young. Call children gullible, or “learning ready,” but their spongelike aptitudes function to spare small and vulnerable creatures the fatal costs of learning through trial and error. “Don’t go near the water,” and especially “Don’t tease the saber-tooth tiger,” are the examples that came to the grandfatherly mind of George Williams.³⁵ One reason television is such a perilous medium is that even infants less than two years old imitate what they see on the screen, yet what appears there is determined by what happens to appeal or to sell rather than by what behavior helped individuals in a particular past environment to survive or prosper.

Few geneticists question the importance of maternal effects or early learning since they know that the course of evolution (used here to mean changes in gene frequency) can be altered by nothing more substantial than a powerful idea acquired early. A Hutterite daughter who imbibes Anabaptist doctrine along with her mother’s milk is more likely to grow up to bear ten children (the average for her group) and be the least likely of any woman in any population ever studied to die without surviving offspring.³⁶ Meanwhile,

another little girl down the way, who grows up convinced of Christ's imminent second coming, and who as a consequence joins a religious community such as that of the celibate Shaking Quakers, decreases her odds of bearing any children at all.

In part II, I will return to what is the most important of all maternal effects in terms of infant survival: a mother's decisions about how much to invest in her offspring, and in some cases even whether to nurture her infant at all. In part III, I speculate about the significance of maternal commitment for what the developing human infant learns about its social environment.

From 1975 onward, sociobiologists began to incorporate situation-dependent phenotypes and maternal effects, along with natural selection, kin selection, and sexual selection, into our understanding of evolution. "Looking to the animals" in this new way made it inevitable that sooner or later mothers would be recognized as playing active and variable roles on the evolutionary stage. But other factors, including new protagonists among the theory builders, sped up the revision. An explosion of field studies by an increasingly diverse group of researchers in animal behavior and human behavioral ecology unveiled previously unimaginable variation in the natural history of mothers.

Unimaginable Variation

If there were one level of feminine incompetence as strict as the ability to count three and no more, the social lot of women might be treated with scientific certitude. Meanwhile the indefiniteness remains and the limits of variation are really much wider than anyone would imagine from the sameness of women's coiffure and the favourite love-stories in prose and verse.

—George Eliot, 1871–72

The most significant impact of this new [evolutionary ecological] thinking was in its focus on variability . . . in how parents behave and how children fare. . . .

—Jane Lancaster, 1997

Every female who becomes a mother does it her way. From an evolutionary perspective, what mothers have in common is their high and quite certain degree of relatedness to each infant. What varies are the costs that caring for a particular infant will impose and the potential payoff in terms of that offspring's prospects of translating her investment into subsequent reproductive success. So far as natural selection is concerned, mothering is anything and everything a female does to ensure genetic representation in subsequent generations. Narrower prescriptions implying that every mother would be a fully committed, "loving" mother were just somebody's wishful thinking.

When sociobiologists followed the advice of early moralists by looking "to the animals," they did so not in search of moral guidance but to learn *why* creatures behave as they do. Instead of natural laws demonstrating how mothers *should* behave, nature yielded a series of contingent statements. Whether or not a female produces offspring depends on her age, status, and physical condition. Whether or not, and how much, she commits to such offspring as she bears depends on her circumstances, and—in cooperative breeders like humans—on who else is around to help her.