

## Chapter 16. Genes, Environment, and Development

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### **Genes, Development, and Behavior**

We have already seen how single genes can have profound effects on what are considered to be highly integrated behaviors. The example of the *fosB* mutation in mice (Chapter 2), which is a key gene in the gene cascade for nurturing behavior, exerts its influence on a large number of traits via pleiotropy. It is simplistic to assume that a single gene governs all of the complex actions of the nurturing mother mouse. Many genes govern maternal care. However, a single gene may be instrumental in altering the cascade of events that lead to nurturing. Similarly, a single gene affecting levels of testosterone might have a profound effect on the phenotype and exert its influence on a suite of traits by virtue of the multitude of effects that T has on a variety of organismal traits such as muscles, morphology, physiology, and behavior.

Simple mutations in key regulatory genes that affect behaviors provide a very simple mechanism that promotes sweeping changes in alternative strategies (Chapter 8). Mary Jane West-Eberhard (2002) has advocated that this kind of mechanism underlies the evolution of developmental patterns in more complex social systems. Rather than reconstructing an entire set of developmental pathways to create a new phenotype, a simple genetic mutation in a regulatory network might alter an existing developmental program in large-scale ways. For example, Andrew Bass speculates that the Type I male of the plainfin midshipman fish is the ancestral form (Chapter 15). Recall the simple pathway: gonadotropin releasing hormone → gonadotropin → gonad growth → testosterone (Chapter 7, 15). A simple mutation in GnRH may have produced the novel Type II males that mimic females. Development of the Type II phenotype may have simply short-circuited the Type I phenotype, in that Type II males resemble females in many ways. In most vertebrate species, the female morphology is considered the **ground state** (default plan) upon which additional hormones (e.g., T) might exert their organizational effects. In the absence of *sry*, a key vertebrate gene for gonadal development, individuals will resemble the female body plan.

We have clear examples of the role of a gene in affecting behaviors, and we can see that they do not act in a simple ways. Rather they act in an

epigenetic process in which the genes trigger the building of complex structures (e.g., endocrine glands, the circulatory system) that then regulate the development of behaviors (e.g., see spadefoot toads at the end of Chapter 2). There is no single gene that controls the development of the hypothalamus-pituitary GnRH-gonadal regulatory axis. A gene complex is required to build the HP gland. A separate gene complex is required to build the gonads. These glands must act in a coordinated and a concerted fashion. Therefore, such functional integration between the different components of the endocrine system must arise from correlational selection. The regulation of levels of GnRH and its cascading influences on FSH or LH, must be coordinated with the effects of FSH and LH on steroidal expression in the gonads. The steroidal expression in the gonads must likewise be coordinated with ERE gene promoters that govern gene transcription and translation in various parts of the body (brain, secondary sexual structures) to effectuate an adaptive phenotype in males, females, or any alternative strategies that exist in each of the sexes (e.g., sneaker males, territorial males, Chapter 8).

In the brain EREs in various target cells, which have differentiated, may produce an enzyme that metabolizes a steroid hormone to effectuate gene cascades that hasten development of alternative structures (Chapter 14). Correlational selection among the gene complexes generates functional integration of the hormones, the reproductive system, their receptor proteins, and promoter elements on the DNA (the receiver targets) that respond to the sender molecules (hormones). These different sender and receiver systems are clusters of disparate genes in the genome and yet they need to be highly coordinated. These complex issues of proximate mechanism and ultimate patterns of selection are poorly understood and lie at the center of our understanding of the evolution of behaviors.

In this chapter, I explore how interacting animals resemble the signaling molecules of development. Hormones travel to hormone receptors and effectuate an endocrine response in receiver genes such as gene transcription. Animals travel and move. They come into contact with other animals, signal, and thereby invoke a behavioral response in the receiver animal. These behavioral responses are coordinated by the action of ancestral patterns of selection (see Chapters 3, 4, 5, 6, 7, 8, 9,

10). These simple interactions are built into more complex multi-animal interactions that can lead to the emergent properties of genes and gene interaction, which we call social behaviors. Therefore sender-receiver interactions of genes are conceptually unified with sender-receiver interactions of animals. These behaviors are innate and coded by genes.

### **Behavioral programs of the endocrine and nervous systems**

Ethologists have always had a fascination for genetically programmed behaviors. The difference between males and females within a single species illustrates such effects because the genetic basis of sex determination and differentiation is well characterized (Chapter 15). Many behaviors are thought to "hardwired" and ethologists have termed such behaviors as **innate**. Arguments made by some ethologists (e.g., Lorenz) contend that the basic neural circuitry for receiving stimuli in the early stages of development control much of an animal's behavior. To be sure, a young animal does not have much experience. There is no need to learn every behavior; the animal could be born with an "**instinct**" for many seemingly complex behaviors.

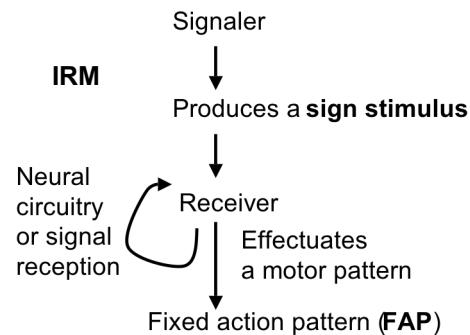
In contrast to this view, the students of the field of behavioral psychology contend that environment plays a major role in learning behaviors. They certainly do not discount the existence of innate behaviors, but that the environment plays a major role. Differences between ethology and animal psychology led to a debate on the causes of behavior that has been captured in the phrase "**nature versus nature**". Are the behaviors seen in organisms a product of their genetic background, or their environment? We will not fully resolve this debate in this Chapter (16), but will continue with the debate into Chapter 17.

As we will see, despite the controversial nature of this debate, it is not a question that can simply be answered in terms of either nature or nurture. Behavior can be the result of a complex interaction between genes and the environment. We have already seen how bird song is developed through a male hearing his own voice, thus a male must receive at the very least information from himself to produce a song. The song that he produces is quite poor unless he has been exposed to the species typical pattern during the critical period for learning song.

Thus, the neural circuitry can be affected in interesting ways and experience can profoundly shape the "wiring diagrams" for behaviors. In this chapter, we will explore some of the classic ideas on nature and nurture, and the role of the environment. In this Chapter, I explore innate behaviors, which can also be modified by experience. Innate behaviors can be built into complex behaviors via interactions with conspecifics.

## Stimuli and Innate Behaviors

Ethologists speak in terms of sign stimuli, innate releasing mechanisms, and fixed action patterns. A **sign stimulus** is an external signal that triggers a specific response from an organism. The response is triggered by the **innate releasing mechanisms (IRM)**, which is a neural circuit for mediating signal detection and effectuating motor actions that result from coordinated muscle contraction. The **fixed action pattern** is the set of innate behaviors that are triggered by the IRM. An example of an IRM was detailed in Chapter 14, where I described the visual system of the feeding toad. From what we know of these neural circuits, it is clear that such circuitry can be built up from genes, but this again requires epigenetic processes involved in neural development (see Chapter 17).



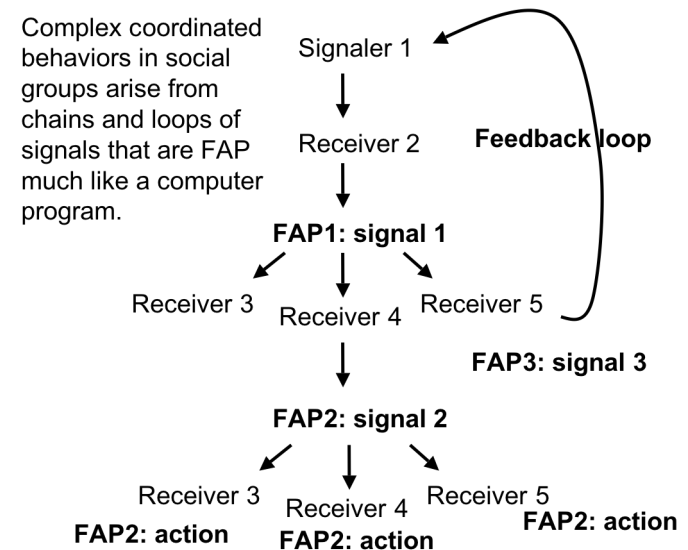
## Sign Stimuli

A classic [sign stimulus](#) (see 3 Meg video) triggers the courtship display of male three-spined sticklebacks. The enlarged belly of a female triggers the zigzag dance in male sticklebacks and this dance is used to entice the female to enter the nest that the male has built. In this video, the male is more likely to court a super gravid dummy (a more extreme or supernormal sign stimulus) than the normal gravid dummy. Jenny

Jenkins of Indiana University set up this encounter of a male and two dummy females, which differ in the degree of belly enlargement.

## Innate Releasers and Fixed Action Patterns

In the case of the distended fish belly simulating a gravid female (above), the male enters a fixed action pattern (FAP) of courtship in which he does a zigzag dance with his head down and approaches the female then circles back to point out his nest. The FAP response is highly stereotyped to the point of being repeated over and over and over.



**Figure 16.1. (Top panel)** The signal, the innate releasing mechanism (IRM) that receives and integrates the signals, and the fixed action patterns (FAPs), comprise the basic unit of signaler-receiver communication for the molecules governing behavior. These FAPs can be assembled into more complex networks among individual organisms of a colony, or between males and females during a mating ritual (Chapter 10), during male-male conflict in stereotyped displays (Chapter 8), or in fact any form of animal communication (Chapter 13). In this chapter, I elaborate how complex colony behavior is built up from a simple elaboration and iteration of connected loops of IRMs and FAPs with feedback.



**Figure 16.2.** The brain of *Tritonia gilberti*, which contains unusually large neurons (outlined), was used to investigate the neural bases of one of the very first FAPs to be identified. The sign stimulus is touch or an irritant applied to the body, which then induces a FAP of swimming in this marine mollusk. The electrical activity or recordings of nerve impulses in A is from an intact swimming animal induced to swim with an irritant, B is from an animal whose neurons in the group of cells circled in the top panel were electrically stimulated. C and D are enlarged versions of A and B. (from Dorsett et al. 1969).

The neural bases of FAPs were isolated fairly early on (e.g., Dorsett et al. 1969, Figure 16.2). Escape behaviors of many animals including the marine mollusk, *Tritonia gilberti*, are classic FAPs. Another escape FAP

was described in Chapter 8 for the crayfish. The molecular bases of the crayfish FAP have been isolated. Changes in serotonin receptors at nerve cell gap junctions result in **synaptic plasticity**, thus FAPs can change in response to social experience. See Chapter 8 for a description of the crayfish FAP that is used in escape behavior during male contests.

FAPs are often involved in aggressive encounters, such as among male sticklebacks. If a small amount of red is added to the belly of a dummy stickleback, the males will engage in a stereotyped attack response -- the **circle fight posture**. This FAP is only the beginning of what may escalate into a battle between sticklebacks. Each step is governed by IRMs and FAPs. Tinbergen discovered the red signal in a serendipitous series of observations (Bill Rowland personal communication). Tinbergen noticed that a male stickleback in one tank would rush over to the window and display aggressively at about the same time every day. One day Tinbergen realized the source of the stimulus that triggered the FAP. The local postal trucks were bright red, and the male was responding to the red image of the postal truck seen off in the distance.

I have my own experiences with similar phenomena in a different species, the redwing blackbird, *Agelaius phoeniceus*. While commuting to my study site at Los Baños Grandes from Santa Cruz, I pass by many marshes where redwing blackbirds set up breeding territories. The males defend their territories in the rushes from other male conspecifics. One day I was driving behind a red Jeep and I noticed that the male red-wing blackbirds would turn to the oncoming Jeep and effectuate a stereotyped display with their head down, wings spread to the sides, and with the red patch on their own epaulet displayed prominently to the oncoming Jeep. They began to sing and even launched a mock aerial attack.

The simple kinds of FAPs can also be used to generate highly coordinated behaviors among cooperating individuals. At the level of a colony of insects, chains and loops of different signals, which are the FAP response to another earlier signal in the chain, can be used to generate very complex and coordinated behaviors. We will explore this complex chain of events in simple animal societies later in this chapter. We begin with the earliest innate response of early life, imprinting, in which a signal can be stored in memory as a **neural template**.

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## Imprinting

**Imprinting** is a process that usually occurs within the first few hours of birth or hatching. During these early stages, offspring will imprint on a nearby object that is animated. In some species, the imprinting might involve auditory cues found in the female's calls (e.g., sea lion females). Some birds will literally imprint on moving stuffed objects. After such **filial imprinting**, the offspring will follow the mother, or respond to the mother's calls. Konrad Lorenz had geese chicks imprint on him (he was the first thing they saw). These goslings followed Lorenz everywhere. Lorenz elaborated on the various forms of imprinting.

**Sexual imprinting** is a special kind of imprinting in which offspring imprint on members of their own sex, and when the offspring mature, they prefer their own species. However, mistakes occasionally happen in the wild. We have already seen an example of sexual imprinting in Chapter 5, where I described song learning in birds for the first time with the example of imprinting and misimprinting in Darwin's finches.

Recall from this example that a tutor's song is necessary for recognition by an individual of its own population -- [deme recognition](#) (Chapter 5). There are several species of Finches on a single island in the Galápagos. Two finch parents participate in the rearing of the young. The father's song is usually learned by the male and female offspring. This song is important for species recognition. Occasionally, the father dies, and the chicks only hear a neighbor's song. If the neighbor happens to be the same species there is no problem. If however, the neighboring birds are a different species of finch, the fatherless offspring learn its song and attempt to court or mate with the wrong species when they mature.

In general imprinting in animals allows them to build long-term associations for signaling to key individuals in the social group. Imprinting is a form of synaptic plasticity, but one in which the neural template, a large block of storage neurons, retains the "signal image" for a long period of an animal's life span.

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## The Environment and the development of behaviors

Innate behaviors appear to be coded by relatively simple neural circuits, however, the motor circuits that they trigger are quite complex. The only external event that is required is the sign stimulus, which acts as the innate releasing mechanism to generate the fixed-action pattern, which is then acted out by the animal. In this section, we will look at behaviors that are modified by the external environment to an extreme degree.

The first example, that we will consider is the case of worker bees and ants, their caste determination mechanisms, and the rules that they have for worker allocation. In these groups, determination of the different worker castes is modified by inputs from the **environment**. The environmental inputs are quite varied and include temperature, hormones provided by nurse workers, or even the egg size of the female. A second behavioral issue for social insects involves the coordination of tasks in the colony. It is often argued that social hymenoptera colonies are some kind of super organism. There are no decision makers in a colony, rather colonies coordinate their activities by their interactions with other colony members and follow very simple rules that govern the outcome of interactions. Such individual behavior leads to an "apparent coordination" or self-organizing property to the colonies. To understand the workings of such insect societies, we will also consider how:

1. various castes in the colony are determined,
2. tasks are determined, and
3. tasks are coordinated.

The second example that we will consider is the case of song production in birds in which song learning is modified by the **social environment**. We will first consider classic songbirds in which tutor birds are present during the critical period. In the case of classic song learning, the young birds (male and female) usually require a **male tutor** for learning the species typical song. We will then consider the unusual case of the cowbird that is parasitic on the parental efforts of other birds. The cowbird chicks are reared in nests with an inappropriate tutor so there

must be some mechanism for generating species typical song in the absence of a suitable tutor. In studying the cowbird, it is clear that the development of song in young male birds also requires **interactions with the females**. Even though females do not sing, they still give the male feedback during song learning. These examples span the breadth of the two mechanisms that modify innate behavior -- genes and culture.

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### **Caste Determination and Task Allocation in Hymenoptera**

The social hymenoptera form some of the largest and most complex societies in the animal kingdom. They accomplish many of coordinated tasks without a defined leader. To be sure the queen of the colony provides some "guidance", but only to the immediate workers who tend to her egg making machinations. As she drops eggs, the workers scurry about to bring the eggs to a nursery. The queen can produce fertilized or unfertilized eggs and this for of [haplodiploid sex determination](#) (Chapter 2) leads to either male or female offspring.

Besides sex determination, how are the foraging efforts and subsequent tasks allocated in such colonies of insects? In many societies there are also castes in which the sterile workers have strikingly different morphologies, which have been suggested to be optimally designed for certain tasks. For example in army ants there are small attack/foraging ants, and larger sub-major and major classes. Surprisingly, the smaller ants do all the attacking of prey, but do so in extremely larger numbers. The sub-major and major classes of ants are specialized for hauling the large subdued prey items back to the bivouac along "super highways" at high speed, which comprise ant autobahns.

#### **Where do such castes come from? Royal jelly and Caste determination.**

Genetic control of caste determination would, in principal be very difficult ([but see a counter-example that is discussed below](#)). The reason has to do with the limited genetic material upon, with which the colony is founded. If there were some kind of selection process, in which castes of genetically determined types self-assembled into each individual's

role, it could be possible to have genetic determination of some kind. Indeed, the haplodiploid system per se reflects a genetic form of determination in which fertilized eggs (2N) can develop into workers or the queen, while unfertilized eggs (N) develop in males. In this case the queen and workers carry out the selection (see Chapter 11 on conflict).

To solve the issue of caste determination, a variety of interesting environmental influences have evolved. The breeding and non-breeding castes are largely environmentally determined, through interactions with the other colony members. For example, in the case of the queen bee in a new colony, the following events lead to her "coronation". At some point during the reproductive season, the old queen and the workers integrate the information on the colony reserves and a group decision is invoked to form a swarm. The old queen lays special eggs prior to her departure, and the workers tending the several eggs that she has laid puts them in slightly larger brood chambers (e.g., honeycomb cell). The old queen recruits many workers of the colony to join her in establishing a new colony and she leaves the old colony without a queen. The now queenless nursery workers are not receiving pheromonal cues from the old queen. They begin to produce a **royal jelly** that they feed to the several queens that are growing into larvae in the queen rearing chambers (Figure 16.3, life cycle of the honey bee). The royal jelly contains the hormones that trigger the development of the ovary, which occurs via effects of a potent insect hormone called **juvenile hormone**.

#### **Social selection and sister assassination**

The queen develops into a fertile form rather than just a sterile worker. As soon as the first larval queen hatches, she moves to the other royal chambers where her sisters are about to hatch. She then kills each and everyone with her functional stinger (recall that workers have a stinger that stays in the prey, the queen possesses a multi-use stinger). This queen then embarks on a mating flight and mates with one to several males (a male drone is the product of an unfertilized egg, see Chapter 4). After this mating flight, she returns to the colony and begins to lay fertilized eggs that develop into new sterile workers.

In the case of queen determination, the stimuli that re-organize the new queen's morphology and behavior come from the environment, her sisters or aunts who feed her the royal jelly. As the bee develops in the "nursery", special accommodations are arranged for the larger bodied "queen" larva, pupae, and eclosing adult. The chamber in which the egg is deposited is made much larger again an environmental effect that enhances the queen's larger-bodied phenotype. As the larva develops, nurse workers provide a special royal jelly, which promotes ovarian development, an event absent in the development of sterile workers.

A profoundly important instance of **social selection** (see Chapter 4) occurs when the new queen kills her sisters. The first queen to hatch undoubtedly carries genes for rapid development. These genes for rapid larval development are highly functional from the point of view of colony efficiency, compared to the later hatching sisters that she kills. Therefore, the process of queen selection involves an important component of self-selection with the group of individuals that have the potential to develop into a queen.

Thus, queen determination involves two kinds of environmental inputs; one is purely environmental, while the other generates a selective event that shapes the colonies genes:

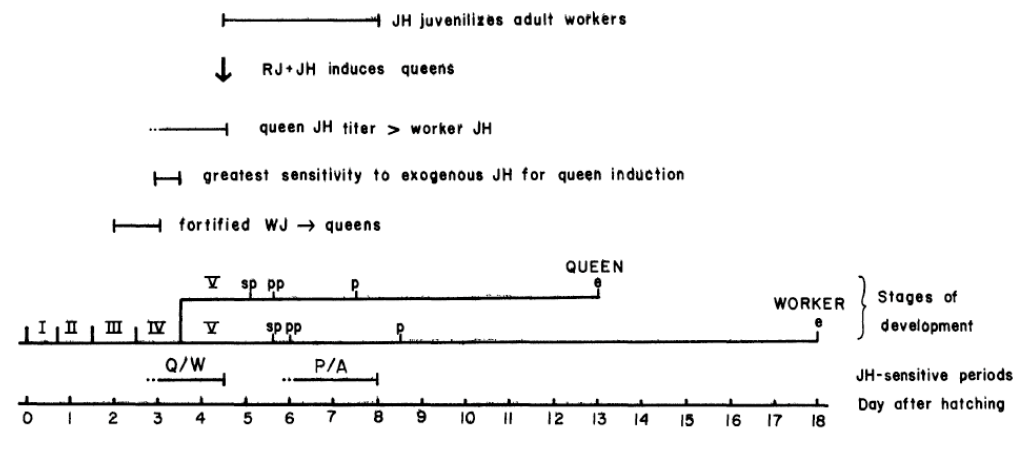
- 1) **A developing larva's sterile sisters provide royal jelly -- an environmental input on the development of fertile queen versus sterile worker behaviors (note also the enlarged cell).**
- 2) **The social selection by queen killing other queen's has an important component of queen killing shapes the genes of the new queen and all new workers produced by the colony.**

The colony also has the capacity to recover from an event that leads to the untimely death of the queen that does not leave an obvious successor. If a queen dies without leaving a group of eggs from which the heir apparent is self selected, then:

- 1) the workers in the nursery immediately enlarge the brood chambers of several newly laid eggs,

- 2) the workers begin to develop royal jelly, and then begin feeding the eggs in the enlarged chamber the royal jelly
- 3) a queen develops from eggs that were otherwise destined to be workers (in the absence of enlarged brood cell and royal jelly).

**Figure 16.3.** The development of castes in honeybees is governed by two important endocrine factors, royal jelly [RJ] and juvenile hormone [JH]. The role of hormones in insect development and the nuclear receptors for JH are discussed in Side Box 16.1. JH contributes to queen characters in bumblebees, honeybees and also stingless bees, but genetic factors have also been strongly implicated in stingless bees (from Nijhout and Wheeler 1982). RJ refers to royal jelly, WJ refers to worker jelly, JH refers to Juvenile hormone.



### Task Allocation in the Honey Bee

The maintenance of the hive entails a number of tasks. In bees, there is generally not the sophisticated development of different castes to carry out the various tasks of hive maintenance. There are just three morphological types:

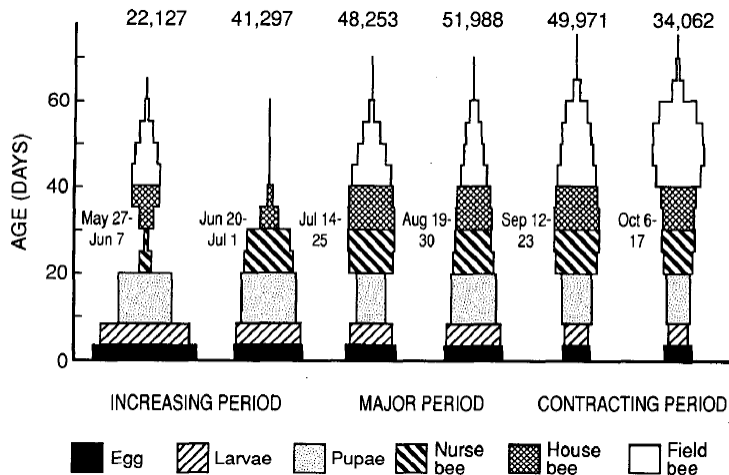
1. The queen (diploid –royal jelly)
2. the male drones (haploid)
3. the sterile female workers (diploid – no royal jelly).

For early studies of marked bees, it was clear that an individual worker performed a single task over the course of several days, seemingly specialized in one of the following roles:

1. **nursery** -- bees that tend to the needs of developing larva
2. **house bee** of the honey comb and food larder -- responsible for comb maintenance, and caching of honey in the combs
3. **forager** -- individuals that go foraging to discover food sources
4. **scout** -- individuals that seek out known food sources.

Over the course of several weeks the worker might move on to the next task in the sequence. The relative proportion of individuals that are allocated to each task varies with the season (figure 16.4).

How does specialization in such roles come about? Three theories have been posited to explain the caste determination in bees: 1) foraging for work, 2) genetic determination, and 3) age-dependent (hormone dependent) programming of behavior.



**Figure 16.4.** The relative proportion of each caste in a typical honeybee colony changes during the reproductive season (from Robinson 1982).

### Environmental determination of tasks: "foraging for work".

One theory (Franks and Tofts 1992), **foraging for work**, holds that these defined developmental roles are largely due to a random process of job selection that is spatially correlated with the center of the hive – the nursery. Because all bees are born in the nursery, this is the first environment that they encounter. If there is a simple rule:

- that workers look around their local environment, and begin working on tasks that need to be done
- thus, young newly born workers will immediately take up tasks in the **nursery**.

As a worker toils away at its task, by chance, all tasks may be filled in the nursery. The worker moves outside of the nursery arena to "forage for more work". The next place she would encounter is the outer hive, where maintenance tasks might be open for her working instincts. Eventually, these individuals begin wandering and interact with the workers in the **larder** to get food for unoccupied and thus available for her to fill. During her long life (3-4 weeks) she would continue with this task until displaced yet again to forage for new tasks. After performing tasks in the larder, the worker begins interacting with **foragers** and assumes such tasks, especially if younger workers that have now moved into the larder displace her. Finally, the foragers interact with the **scouts** and eventually assume such tasks. The most complicated tasks and thus the highest level of cognitive function (Chapters 6, 12) requires the old scouts, who serve as the **distributed memory bank** of the colony.

Exposure to new environments and opportunities for work leads to the development of specialization with age. The task allocation is simple, forage for work. If no work is in the immediate vicinity, they move a little farther from the center of the hive and look for undone tasks.

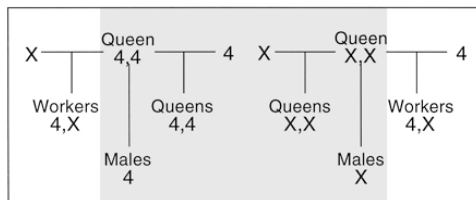
### Genetic determination of tasks.

There are other theories to account for the correlation between the age of a bee and the various tasks that occur further and further from the hive. This could occur by selection. Only those workers with the ability to



avoid predators survive to move on to the scout caste. Even though workers are very similar to one another and their relatedness is very high ( $r=0.75$  vs. the usual  $r=0.50$  for sexual offspring), they do receive different material from their female parent, the queen. The queen might have mated with several males (polyandry) further enhancing the genetic diversity of the hive. These subtle genetic differences might pre-dispose them to different tasks in the hive (e.g. nurse, scout, morgue vs. guard).

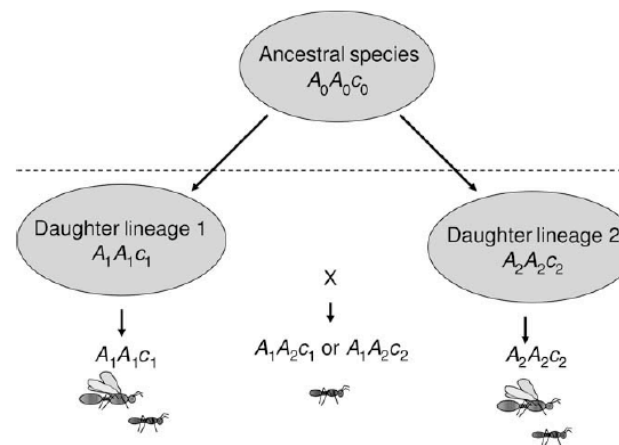
Volny and Gordon (2002) have recently described a linkage map analysis using microsatellites, which identifies a gene (in tight linkage with one microsatellite) that determines worker vs. reproductive castes (Recall the microsatellite linkage analysis of the OBY color locus in lizards and self-recognition factors for color, Side Box 4.3, Chapter 4). A synopsis of ant pedigrees reveals that several loci at the microsatellite locus seem to be tightly associated with queen (and male) production (Fig. 16.5). Volny and Gordon indicate that if a female with allele 4 is to produce both workers and gynes (e.g., reproductives), she must be polyandrous. She must for example mate with a male that is carrying 4, and she must mate with another male that lacks allele 4 (e.g., 2, 10, or 12). If a female does not produce workers, she will not be able to establish a colony, thus the allele 4 is maintained by negative frequency dependent selection. Queens have to mate with both genotypes to produce workers, otherwise they only produce workers (and their lineage dies out, or they only produce gynes and their lineage dies out for lack of workers in the colony that can do all the jobs).



**Figure 16.5.** An example of genetic determination of castes (queen, male versus workers) in the harvester ant, *Pogonomyrmex barbatus*. Shaded areas represent matings from which workers will not develop. Allele 4 from the queen generates only reproductives. Allele X represents either allele 2, 10 or 12, but never allele 4 and 6, which yield gyne determination (from Volny and Gordon 2002).

### Cytoplasmic factors and epistasis in queen determination

An interesting mechanism of epistasis (Linksvayer et al. 2006) has been suggested for evolution of genetic caste determination (GCD) from an ancestral state of environmental caste determination (ECD). In the example of genetic determination of morphs of isopods (Chapter 2), I mentioned that **cytoplasmic factors** are involved in determination of male strategies. The most obvious way to generate **cytoplasmic effects** is via an interaction between nuclear genes and genes located on mitochondria. Mitochondria are only cytoplasmically inherited from the mother (in most organisms). Thus the genetic signature of a **cytoplasmic factor** is an asymmetry in the way genotypes develop from genes inherited from the dam versus sire. The pattern of inheritance in *Pogonomyrmex* (Fig. 16.5) suggests that there are two nuclear lineages. Hybrids (either hybrids between species, or hybrids between lineages within a species) develop into workers but crosses within a lineage develop into gynes. Each colony consists of a single mitochondrial lineage and is derived from a single queen. Thus the pedigree data are consistent with GCD due to between-species hybridization, either due to an ancient hybridization (Helms Cahan and Keller 2003), or of ongoing hybridization or introgression (Anderson et al. 2006). Lineages with GCD could be considered a type of workerless social parasite, with the “host” being the alternate lineage or species. Workers are provided when this **slave-making queen** outcrosses to the host lineage or species (Julian et al. 2002, Umphrey 2006), but she also needs to mate with her own type to produce new gynes.

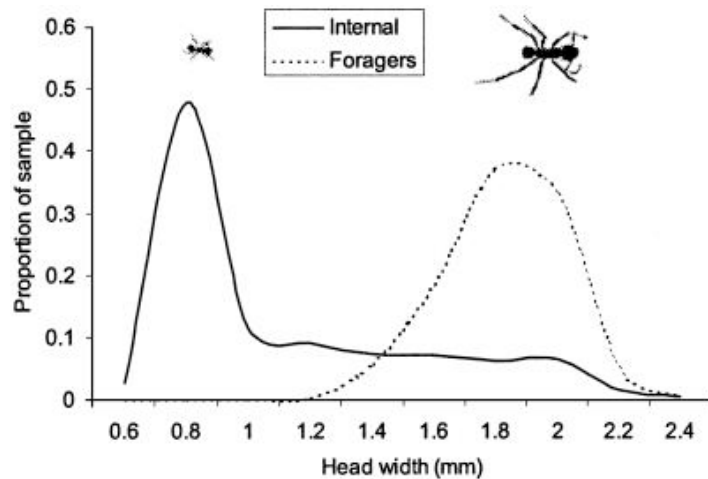


**Figure 16.6.** Cyto-nuclear epistatic model of genetic caste determination, GCD. The ancestral species is fixed for allele  $A_0$  at the nuclear locus A, and for allele  $c_0$  at the mitochondrial locus c. Daughter lineage 1 is derived from the ancestor by fixation of the allelic combination,  $A_1c_1$ , which is introduced by mutation into a population and subsequent fixation occurs by selection and random genetic drift, which is

facilitated by inbreeding. Similarly, daughter lineage 2 is derived by fixation of the allelic combination  $A_2C_2$ . Colonies from lineages below the horizontal dotted line express genetic caste determination, while those above the dotted line express environmental caste determination. Females derived from inter-lineage crosses have disrupted gene combinations ( $A_1-c_2$  or  $A_2-c_1$ ) and develop into workers. Females derived from matings between males and females from the same lineage possess coevolved cyto-nuclear gene combinations ( $A_1-c_1$  or  $A_2-c_2$ ) and can develop into gynes or workers but may have gyne-biased development (Linksvayer et al. 2006).

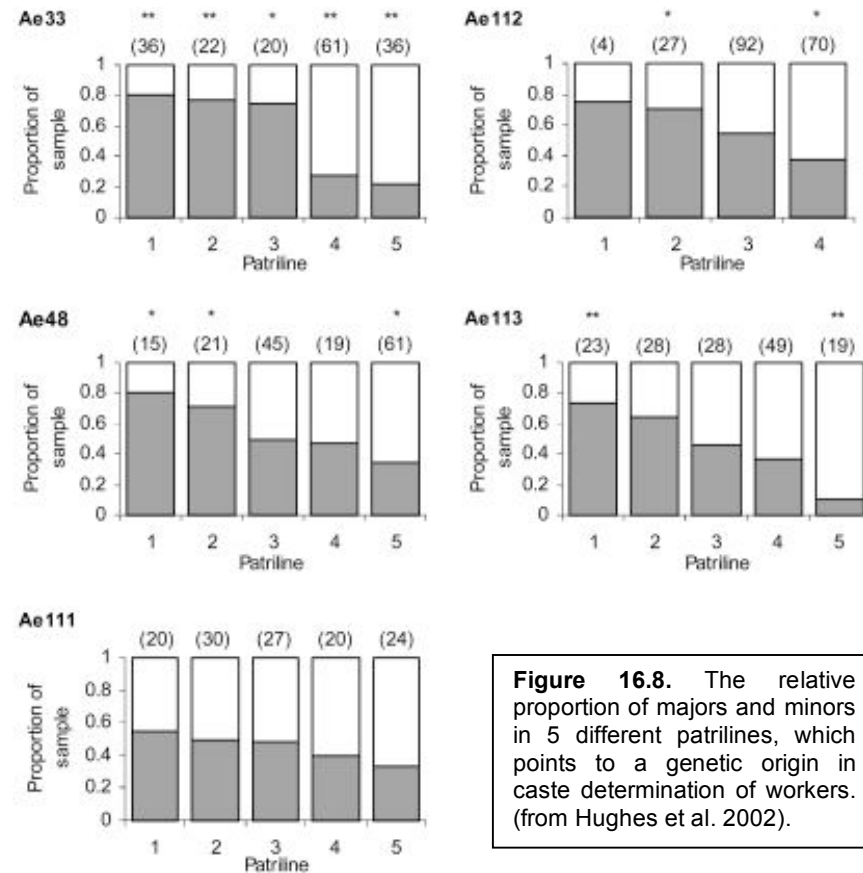
### Evidence of genetic differentiation among worker castes

The case of work/queen determination in *Pogonomyrmex* appears to have arisen from a selfish cytoplasmic gene that corroborates with a selfish nuclear gene to alter worker determination. A convincing example of true genetic determination is best drawn from castes that only develop into workers to rule out such selfish gene interactions. Leafcutter ants appear to have a case of such worker-based genetic determinism. The head width of workers that are internal to the nest is much smaller than workers that are involved in foraging tasks outside of the nest (Figure 16.7).



**Figure 16.7.** Head width in a size polymorphism of leafcutter ants. The internal workers or **minors** are engaged in tasks of fungal gardening and nest maintenance, while the foragers or **majors** are involved in the actual process of cutting and hauling leaves to be used in fungal gardens. (Hughes et al. 2002).

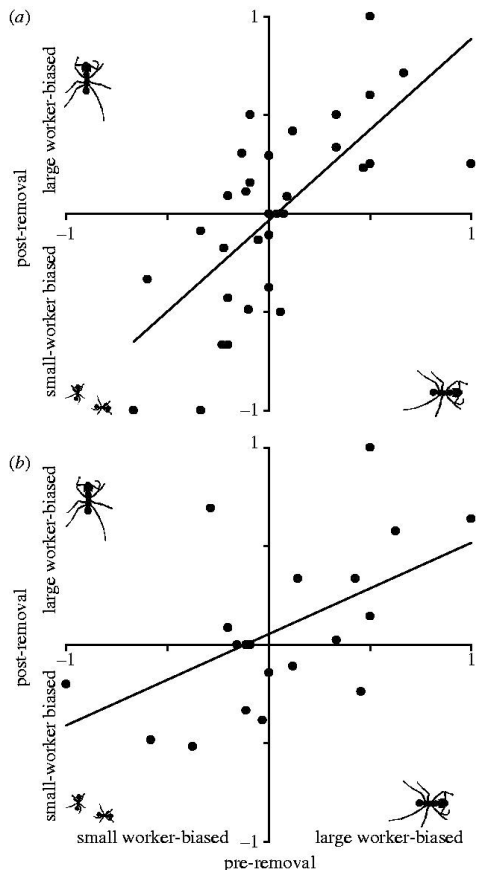
Hughes et al. (2003) carried out a pedigree analysis of the workers produced by different patriline and found that there were consistent differences among patriline in the relative proportion of the minor and major workers, which were observed in 5 different colonies (Fig. 16.8). Therefore a genetic factor associated with development of major and minor workers must be in some way linked to these patrilineal effects. One view is that these males carry alternative genes for development, which females choose to produce a balance of workers of the right size to produce an optimally functioning colony. These effects relate to issues of alternative strategy (Chapter 9), mate choice (Chapter 10) and genes that are in ontogenetic conflict in which genes for alternative workers reflect drastically different optima (Chapter 11).



**Figure 16.8.** The relative proportion of majors and minors in 5 different patriline, which points to a genetic origin in caste determination of workers. (from Hughes et al. 2002).

## Plasticity in the ratio of Majors and Minors

In subsequent work, Hughes et al. (2007) carried out an experimental manipulation in which they removed the major worker castes from some colonies (after measuring the characteristic ratio of major: minors in each colony). They found that some of the genotypes destined to minor workers could develop into majors, under this environmental perturbation of the social dynamics of colony (Figure 16.9).

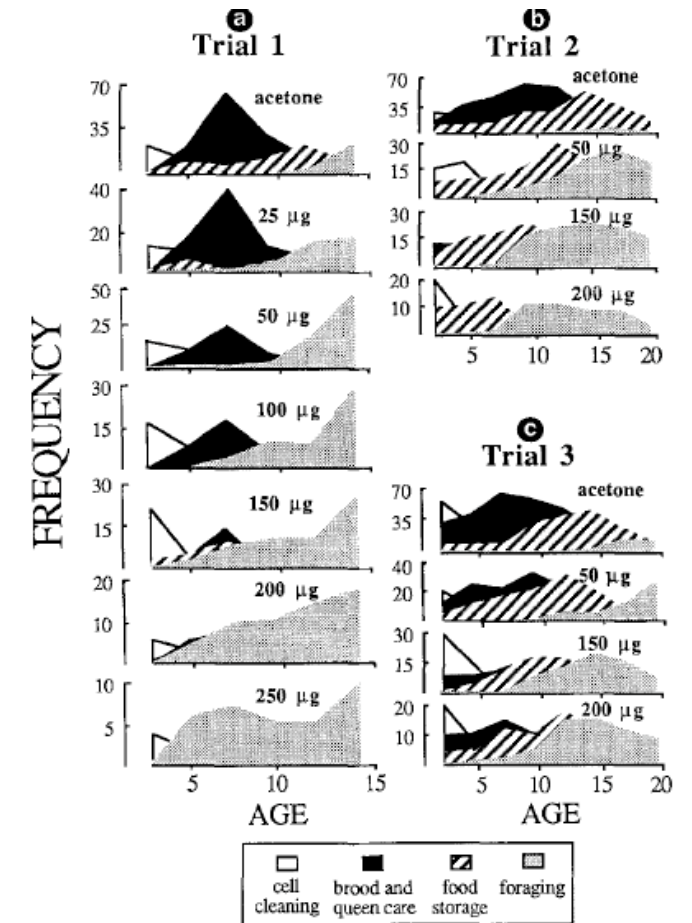


**Figure 16.9.** Caste bias towards major (LW) or minors (SW) for (a) 32 patriline from 5 colonies from which large workers and small workers were removed in equal numbers (LWSW-removal treatment), and (b) for 21 patriline from five colonies from which only large workers were removed (LW-removal treatment). (Hughes et al 2007). Notice the difference in slope between a) and b) and that a) serves as a control in which the proportion of workers remains on the 1:1 line. In b) the slope is significantly lower than 1:1 because more large workers were produced after the manipulation, while in a) the ratio remained unaltered. From Hughes et al. (2007).

**Age dependent determination of tasks.** Yet another theory contends that worker development is programmed by changes that are dependent on age and physiology. For example, a young worker might have a different hormonal profile than older workers. Differences in the internal state of the workers then leads to

differences in behavior. A key hormone might be involved in the progressive change in tasks with age. For example, injecting a "young" nursery worker with **Juvenile Hormone** will cause her to precociously shift her tasks and become a forager. Changes in levels of juvenile

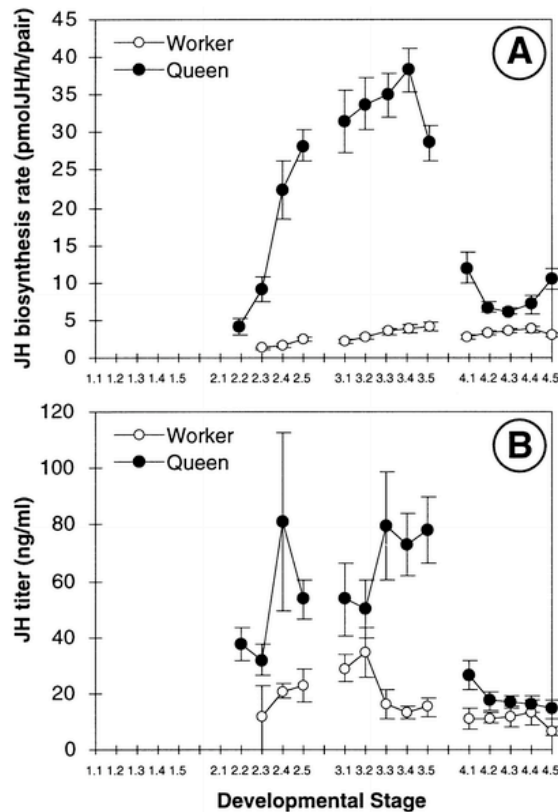
hormone (JH) with age may control task allocation (Robinson 1987). The role of JH has been implicated in altering the development of caste determination at a variety of developmental stages (e.g., egg, larvae, pupa, adult) in various social hymenoptera species (Figure 16.10). Application of methoprene, a JH analogue, accelerates the development of foraging castes in the honeybee relative to the acetone controls (methoprene is soluble in acetone). Acetone controls exhibit normal colony development.



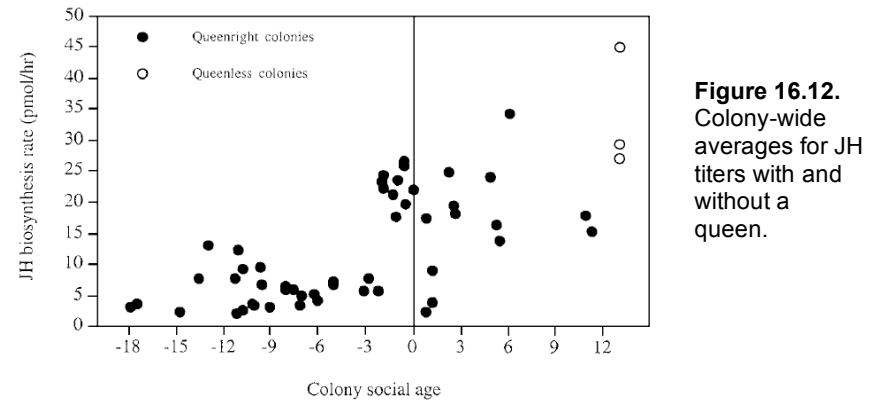
**Figure 16.10.** Development in castes of honeybees under the influence of methoprene a JH analogue (from Robinson 1987).

JH has been implicated in the development of worker castes as well as in the direct involvement of queen determination (Figure 16.3). The role of JH in insect neurodevelopment and metamorphosis is elaborated in Side Box 16.1. The queen clearly has much higher rates of JH biosynthesis than workers over the course of her life (Figure 16.11).

**Figure 16.11.** Rates of JH synthesis in the queens and workers of bumblebee colonies as a function of development stage (from Crani et al. 2000).

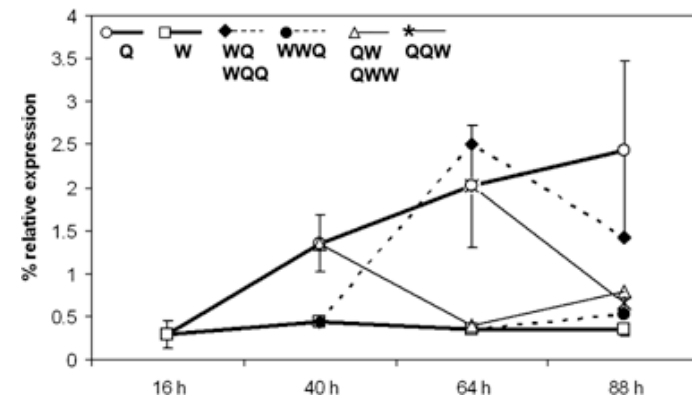


In addition, colonies in which the queen has been removed develop a colony-wide profile of much higher JH titers, perhaps as the various members of the colony vie for transformation into the new queen (Figure 16.12).



**Figure 16.12.** Colony-wide averages for JH titers with and without a queen.

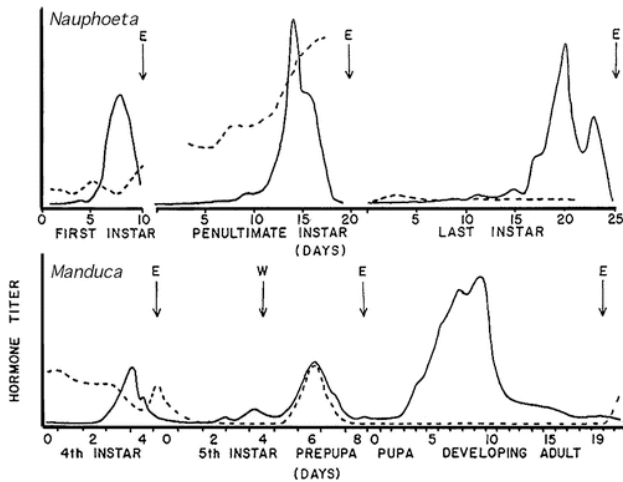
The final component of the puzzle has to do with the signaling pathway for royal jelly, the queen determining substance of honeybees. Recent molecular work (Wheeler et al. 2006) suggests that this potent hormone triggers an insulin-like protein called *AmILP-1* (Fig. 16.13). A molecule in royal jelly, fed by workers to eggs destined to be queens triggers the cascade of changes in JH titer, which alters gene expression (Side Box 16.1 and Side Box 16.2).



**Figure 16.13.** Levels of expression of *AmILP-1*, an insulin-like peptide that is highly expressed in queen larvae. Q and W refer to larval feeding treatments of RJ and WJ respectively. Q and W are controls in which normal development and feeding of RJ and WJ were given to larva. The other treatments reflect varying the amount of RJ and WJ during different stages of larval development (e.g., WQ, WQQ, etc.) (from Wheeler et al. 2006).

## Side Box 16.1. Hormones of insect development

The main developmental hormones in insects are hydroxylated steroid hormones, the **ecdysones**, and the family of sesquiterpene hormones, the **juvenile hormones** (Nijhout 1992). The ecdysones are molting hormones, with the pulses causing events involved in molting (cuticular development, etc.), whereas JHs maintain the insect in its current form as the insect responds to the molting surge of ecdysone. Thus, they have a negative feedback relationship (Fig. 16.14) similar to other vertebrate endocrine hormones. In immature insects, ecdysones are typically produced by the prothoracic glands. The secretory source of the JHs is the corpora allata, a major secretory structure on the insect brain.

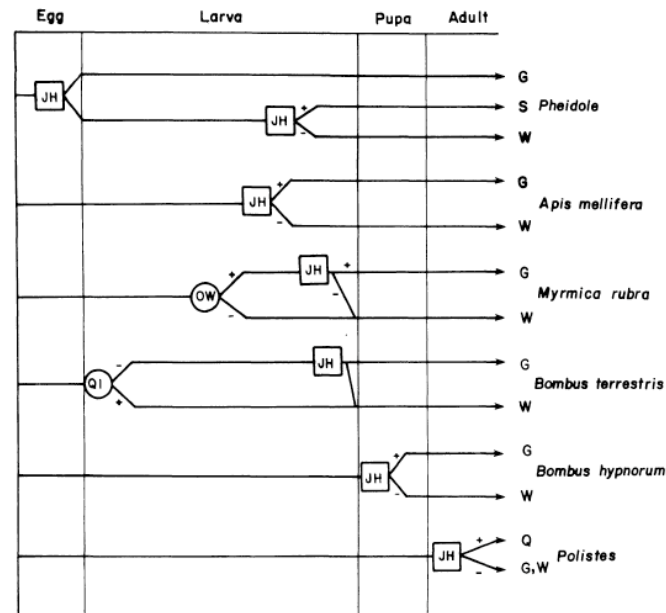


**Figure 16.14.** Juvenile hormone (dashed line) and ecdysone (solid line) titers in two developmental modes of insects, the cricket *Nauphoeta* and the tobacco hornworm, *Manduca sexta*. Crickets are hemimetabolous insects with juvenile instars that resemble the adult. The *Manduca* is a holometabolous insect with a full metamorphosis (from Trumann and Riddiford 2002).

The nymphs of **hemimetabolous** insects (e.g., cricket, grasshopper) and larvae of **holometabolous** insects (e.g., moth, butterfly, beetle, bee, ant) are similar to each other in endocrine interactions between JH and ecdysone. In both molts are caused by ecdysone acting in the presence of JH (Trumann and Riddiford 2002). These developmental modes of insects differ in the endocrine secretion that coordinates metamorphosis (Figure 16.11). In hemimetabolous insects, the JH titer drops to undetectable levels at the onset of the last nymphal stage, and the next ecdysone surge then causes the formation of the adult stage. In holometabolous insects JH declines at some point in the last larval stage.

A small surge of ecdysone terminates larval feeding, and promotes premetamorphic behaviors such as cocoon spinning, and commits larval tissues to pupal development during which the adult body form, which is drastically different from the larval form, is created from imaginal discs, which turn into the feeding appendages, antennae, eye, wings, limbs and reproductive appendages. After transforming to the adult form, JH titres

can slowly increase, and this increase is often associated by dramatic changes in behavior, such as development of the various castes of eusocial bees and ants (Nijhout and Wheeler 1982, Figure 16.15).

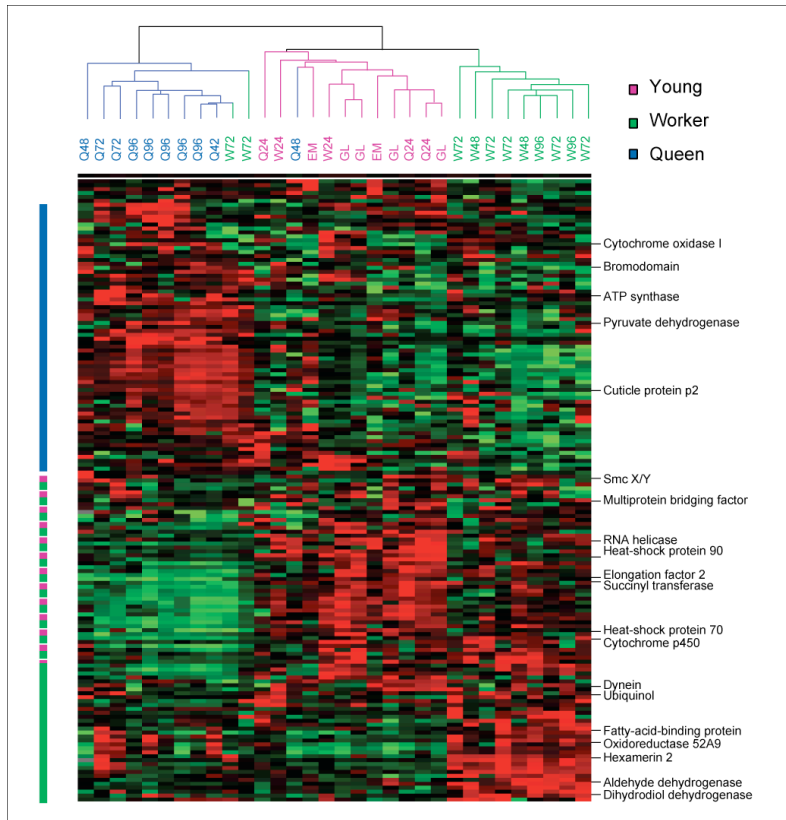


**Figure 16.15.** JH governs caste development in a hymenopteran species (from Nijhout and Wheeler 1982).

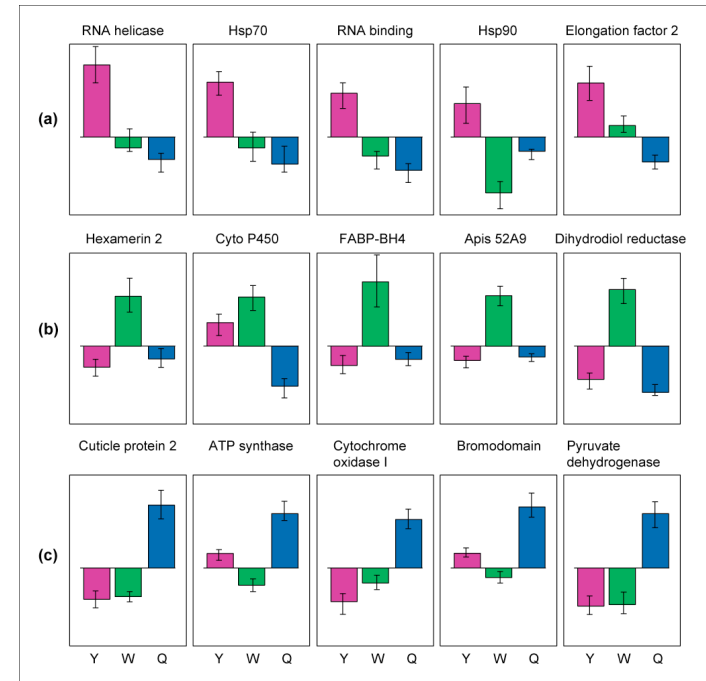
**Nuclear receptors for ecdysone and JH (Trumann and Riddiford 2002).** The ecdysone receptor complex consists of ligand-binding ecdysone receptor (EcR). The heterodimeric partner of EcR (heterodimeric partners have two protein parts) is ultraspiracle (USP), which is conserved in the arthropods. USP is an ancient nuclear receptor whose ortholog, RXR, is found in vertebrates in the form of the thyroid hormone and retinoic acid receptors. *Drosophila* USP binds JH with low affinity, but recent analysis shows that neither JH nor methoprene (a JH analogue) has very high affinity in its ligand-binding pocket. JH acid could fit into this pocket. There is still no clear consensus about the JH receptor. USP is one candidate; yet, it does not fit the criterion of high-affinity binding of the hormone usually considered a hallmark of a hormone receptor. Another candidate suggested for the JH receptor is the product of the *Methoprene tolerant (Met)* isolated from *Drosophila*. In summary, JH and ecdysterone function in similar ways to the key vertebrate hormones that regulate development of vertebrates (Chapter 15).

## Side Box 16.2. Gene cascades of in social hymenoptera

A fairly complete picture of the development of the different castes and even the different FAPs of the social hymenoptera is now emerging. Molecular methods (Evans and Wheeler 2002) allow proteins that differ among castes to be identified. These new methods will eventually allow researchers to pinpoint the cascade of genes that build the different behavioral phenotypes. Evans and Wheeler (2002) use gene arrays during honeybee caste determination to present the first genomic view of polyphenic development (Figure 6.16).



**Figure 16.16.** Gene expression array used in identifying various proteins that differ among castes of social hymenoptera (from Evans and Wheeler 2002). Cluster analysis (top) group specific protein profiles of each caste.



**Figure 16.17.** Genes with different levels of expression can be quantified (Fig. 6.16) from intensity of fluorescence on gene expression arrays into statistical differences between castes (histograms). Levels of expression of various proteins in the different castes of social hymenoptera (from Evans and Wheeler

2002).

Queens downregulate many of the genes expressed by bipotential larvae and turn on a distinct set of caste-related genes. Queens overexpress metabolic enzymes. Workers showed elevated expression of a member of the cytochrome P450 family (implicated in detoxification mechanisms, see Chap. 5), hexameric storage proteins and dihydrodiol dehydrogenase. Young larvae overexpress two heat-shock proteins (70 and 90 kDa), and several proteins related to RNA processing.

Elevated expression of metabolic enzymes by queen-destined larvae reflects enhanced growth rate of queens during late larval development. Many differentially expressed genes are tied to metabolism and cellular responses to hormones, a result consistent with physiological differences between queen and worker larvae. JH and ecdysone levels, which govern expression of ovarian genes (Hartfelder and Engles 2000), are reduced in larvae destined to become workers relative to larvae destined to become queens (Hartfelder and Engles 1998). Gene arrays should allow other proteins to be identified, perhaps including those responsible for generating FAPs that govern interactions among worker castes.

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## Maternal effects in the development of ant castes.

The distinction between queen and worker in colonies of social insects leads to clear specialization for reproduction and colony maintenance. In the case of many species of social ants, the workers are further divided into specialized tasks such as a small general-purpose worker, large worker for hauling large objects (e.g. Fig. 16.7), special warrior castes of various types, including some species in which individuals have a turret on their head and inject noxious chemical warfare toxins and repellents. Underlying selective reasons for such shifts in the number of workers with warrior castes, has to do with colony economics.

### The most efficient colony is likely to leave more descendant colonies.

How do such striking differences in behavior and morphology come about? Such differences clearly must arise very early in development. Holldobler and Wilson (1980) have reviewed the literature and found evidence for at least six mechanisms that contribute to caste determination. I discuss four of these mechanisms below.

**1) Environmental temperature.** Variation in the temperature of development has a dramatic effect on the relative number of workers compared to other specialized tasks. For example, early in the spring, it is necessary to produce more workers because attrition during the course of the winter has reduced the number of workers. By biasing the production of larger numbers of workers at the lower temperatures, the colony will get a more rapid growth spurt. As the temperature heats up during mid summer, and the colony is at close to its maximum carrying capacity, the number of eggs developing into workers begins to taper off. At this point other warrior (defensive or offensive) castes might be produced because workers in the colony encounter more workers from genetically dissimilar colonies. Inter colony wars are about to break out.

**2) Colony Size.** There are clear limits to colony size that are dictated by the distribution of resources. Recall the problems faced by a [central place forager and the Marginal Value Theorem](#) (Chapter 6). There are diminishing returns from too great a travel distance between the colony and the food source. A colony thus has an upper limit to overall size that

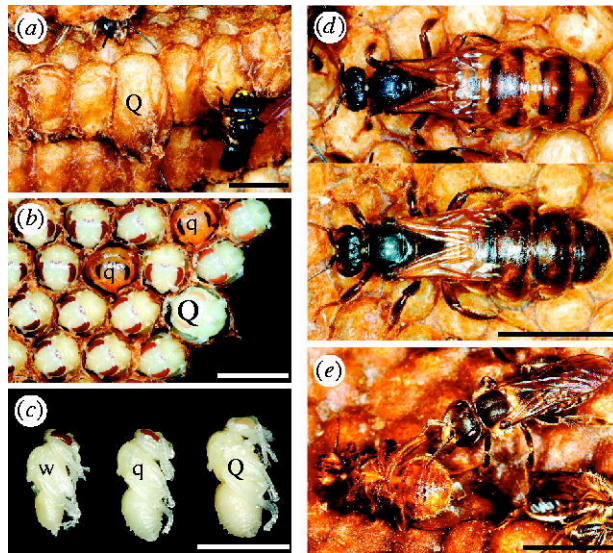
is governed by the marginal value theorem (Chapter 6): the travel costs of individuals to food, the return travel costs (which can be substantial in that an ant can haul 10 times its body weight in food), and the amount of energy required by the colony. Thus, an old colony should be less concerned with expanding its territory, and the number of workers begins to decline with colony age. Defense of the colony from raids that come from adjacent colonies becomes a more important issue. Hence a shift in focus from workers to soldiers occurs in young vs. old colonies.

**3) Queen age.** This shift can also be achieved by some mechanism of worker versus soldier allocation that is tied to the age of the female. As a queen grows old, and as her colony ages, she begins to lay fewer of the worker caste. A young queen should produce many more workers than an old queen. A young queen and hence a young colony must grow rapidly and thus relatively more workers are beneficial. However as a colony grows older and has expanded to its maximum size in both numbers and to its maximum size in terms of the "territory" from which it harvests food, the colony must also consider shifting more members to roles involving colony defense. Hence an old versus young queens produce fewer workers and more soldiers.

**4) Egg size.** Certain of the larger castes come from definitely larger eggs, suggesting that [maternal effects](#) arising from the queen controls development of her offspring. There is no need for a genetic change in the offspring, egg size per se is enough to bias development, subsequent growth, and differentiation along a different pathway and lead to different castes.

## Conflict among workers and queen

A final consideration is important to raise, which revisits issues first developed in Chapter 11 on Conflict. Workers are under constant selection to develop into a queen like morphology and cheat the system. In the stingless bee *Schwarziana quadripunctata*, some individuals reared in worker cells avoid a worker fate by developing into fully functional dwarf queens (Wensleers et al. 2005). Dwarf queens break developmental determination mechanism and develop into smaller but albeit less fecund queens.

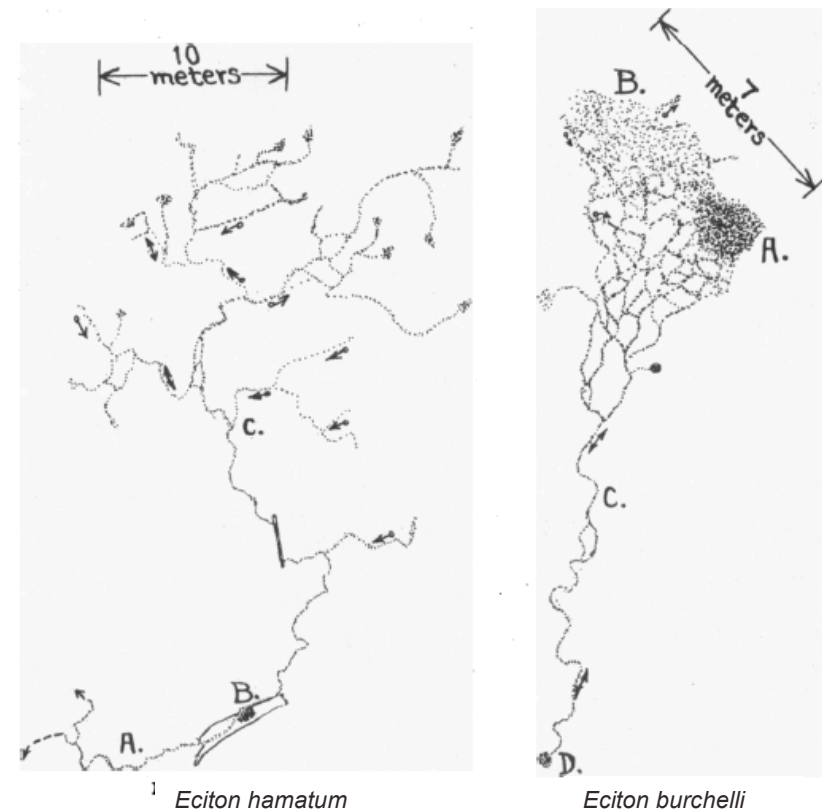


**Figure 16.18.** An example of cheating in the development of queens from embryos destined to become workers. Evasion of socially controlled caste development in the stingless bee, *S. quadripunctata*. (a) Queens are normally reared from larger, specialized queen cells (Q) that are provisioned with a greater quantity of food. The smaller cells in the comb are used to rear workers and males. (b) Here, the comb in (a) has been uncapped to reveal a queen pupa in the queen cell, and worker pupae in most of the smaller cells. However, two of these contain dwarf queens (q), which can be recognized by their smaller heads and eyes and their lack of pollen baskets. (c) The dwarf queens (q) are approximately the same size as workers (w), but are much smaller than normal queens (Q). This shows that the dwarf queens successfully evade an intended worker fate. (d) Like normal queens (bottom), the dwarf queens (top) can successfully head colonies. (e) Workers often discriminate against the dwarf queens. Here, a worker (right) kills a dwarf queen (left) that has recently emerged from her cell. (Scale bars, 5 mm.). (from Wensleers et al. 2005).

### Movement and Mass Action and Foraging Army Ants

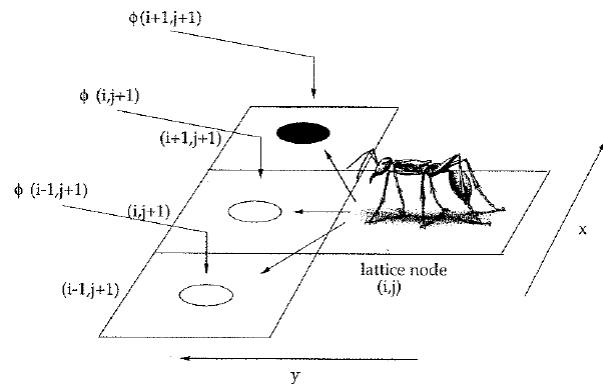
Many authors have advocated the view that the behavioral repertoire and sensory mechanisms of individual workers do not need to be very sophisticated to create the foraging patterns and task allocation patterns seen in such colonies ([see foraging for work above](#)). Indeed the stimulation for mass behavioral actions comes from interactions with other workers. For example, many species of army ants are blind or

nearly blind, and they rely entirely on pheromonal cues for coordinating their activities. The importance of such pheromonal cues is evidenced by the fact that many ants have up to 6 glands for producing these signals. The signaling cues are laid down in extremely minute quantities, but their effects on other workers are both potent and self-reinforcing (e.g., another example of a positive feedback loop).



**Figure 16.19.** Behavioral movements of workers in two species of army ants, *Eciton hamatum*, and *E. burchelli*. The bivouac is located at B for *E. hamatum* and D for *E. burchelli*. In *E. burchelli*, the column of ants is often more concentrated, such as at A and the more diffuse front of B is in the process of a wheeling movement in which the prey located at A is encircled. Army ants form bivouacs that are composed of living colony members for several weeks. The nest is entirely formed from the joined arrays of workers. The army ant *E. burchelli* exhibits a very stereotyped pattern of statary raids in which the angle on subsequent days of raiding is  $123^\circ$  (see Figure 16.17). (from Shneirla 1938).





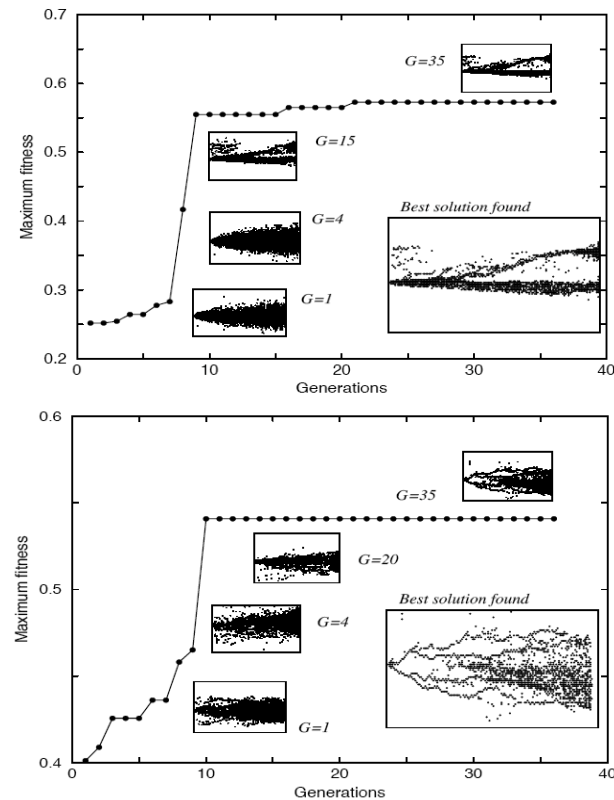
**Figure 16.20.** Modeling army ant movement on a lattice uses a computer simulation called a cellular automata. Cellular automata are extremely useful in analyzing the role of simple behaviors in generating more complex structures including those behavioral processes like cooperation that give rise to socially mediated speciation (see Chapter 19). In this example, the cellular automata is used to analyze optimal patterns of army ant movement based on a simple set of interactions among workers that are based on pheromones. The ant has detected a greater concentration in the right diagonal (Sole et al. 2005).

Consider a simple rule for generating the coordinated movement of army ant columns. Army ants leave on foraging raids early in the morning each day. There is no leader for these ant columns. Rather the individual ants initially appear to mill about randomly, after which they head out in a defined direction. Lets assume four simple rules:

- 1) each ant sniffs for trails and follows the strongest trail,
- 2) each ants lays down its own trail as it follows another trail,
- 3) finally the speed with which an ant moves is proportional to the strength of the pheromonal trail.
- 4) swarm on food, attack and return to nest.

Using these simple rules, let us look at the kinds of tracks that are possible for the ants. Shortly after exiting the colony, a defined column forms and begins to extend out. Many ants are always found at the leading edge milling about randomly (Fig. 16.21). However, the column takes on a defined shape and runs in the same direction. As more and more ants are recruited down a path, they lay down a stronger trail for

the followers. The movement along such columns picks up and they become larger freeways. Smaller routes that do not have as many workers slowly shut down as the larger freeway takes hold. Thus, in close proximity to the colony there appears to be a single well-defined route. As you move further away, a fan like **fractal pattern** is seen in which a single defined route has not been selected. The different patterns of movement in *E. hamatum* and *E. burchelli* appear to be governed by this distribution of their food.



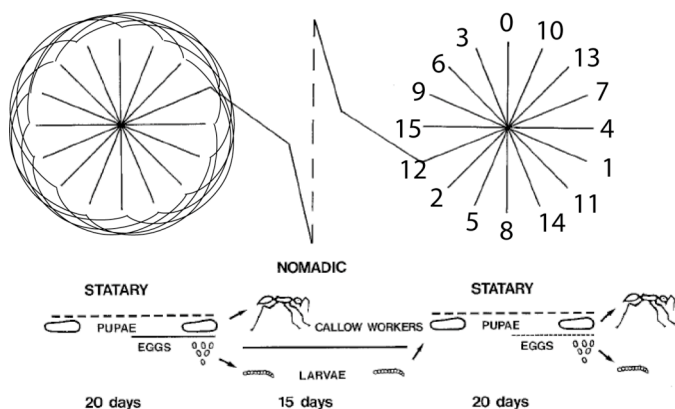
**Figure 16.21.** Results of a cellular automata model of army ant foraging patterns. Solutions found in the case of large but rare food sources. This corresponds to *E. hamatum* colonies. Note the random-walk shape found for small *G* (first generations). The best solution found is consistent with *E. hamatum* raid columns. (Sole et al. 2005). Compare this simulation pattern with Figure 16.19.

**Figure 6.22.** Solutions found in the case of small and frequent food sources, which corresponds to *Eciton burchelli* colonies. Again, the best solution found is consistent with *E. burchelli* raid patterns of a single fanning column. (Sole et al. 2005). Compare this pattern with observed movement in Figure 6.19.

The ants milling about at the many sub-fronts of the expanding column may encounter a vertebrate or an arthropod prey item (Figure 16.15). At which point they swarm, attack, and kill the prey by virtue of their sheer numbers. After the prey has been subdued, the workers bring the item

back to the bivouac. This return movement generates additional activity along the single more defined corridor and further establishes the pre-eminence of a single corridor. All of this apparent "coordinated" activity does not involve any leader. There is no caste that provides direction. The coordination results from the mass action of individual colony workers that are following simple rules of interaction. These external inputs govern the behavior of the colony as a whole.

*Eciton burchelli* also exhibits an extremely interesting raiding pattern from one day to the next in which it changes the angle of the raid by 123°. This angle allows the fan shaped attack column to completely scour a circular area over the duration of the 15 days when the statory phase takes place (the last 5 days are a period of quiescence). Colonies alternate bouts of foraging during **statory** phases with nomadic phases of dispersal. The statory phase is precisely timed to the development of a new crop of workers. The beautiful pattern of **spiral phylotaxis** is extremely well optimized to foraging and consuming all edible food in a circular area. The simplest raid pattern would be to rotate the route by 24°, however, Franks and Fletcher (1983) argue that this would not harvest the prey based as efficiently. By having a period of 5 days and 123° between adjacent raid columns (e.g., 1 vs. 4, Figure 6.22), the colony of ants allow for recovery of some of the arthropod prey base in the intervening 4 days. This would not be the case if the raid were 24°.



**Figure 6.22.** Patterns of spiral phylotaxis (lines that connect successive days left, or numbered days, right) in *E. burchelli* colonies during the statory phase. The 15 days of foraging are numbered (Franks and Fletcher 1983).

## Song Development in Birds

Recall the basic song learning circuit. The [song learning circuits of male songbirds develops in response to early pulses of androgens](#) (Chapter 15). After the early wiring is **activated** by the effects of testosterone, which is aromatized to estrogen in specific areas of the brain, the genes with EREs are expressed, new cells are built and the song learning circuit is ready to begin recording the template songs of a tutor. As we will see, the brain and basic neural circuits that birds develop for producing song are remarkably adaptable and strongly influenced by interactions with the external environment.

We will first review the classic pattern for songbirds in which a **species typical song** is crystallized into a template through a process of learning that entails a tutor, which provides the chick with the template. We will then look at cases in which the template changes during the lifetime of a bird owing to the remarkable properties of neuronal development. The classic paradigm for thinking about vertebrate brain development is that after a certain point, most vertebrates are incapable of developing new neurons -- brains do not regenerate damaged areas very well after trauma and the nerves of the peripheral nervous system do not regenerate very well at all. However, birds have a capacity for developing brand new neurons for learning new song.

### Classic Song Learning

The basic motor circuit for the production of song consists of the higher vocal center (HVC), which connects to the neurons that innervate the muscles of the throat (Chapter 14). Such innervation is not by a direct route, but the circuit passes through two other parts of the brain. A second circuit of the brain, the song learning part, is not directly related to song production because lesions of these circuits do not cut song production. However, if this second circuit is deleted, the young male birds cannot learn song. The songs that they learn are highly abnormal. Males copy a tutor's song during the **sensitive period for song learning** (e.g., 20-65 days in the swamp sparrow), and this song learning circuit is necessary. During this period, the song circuits are growing in size and

the number of cells as the circuit grows via cell division. The male begins rehearsing and practicing its song during the rehearsal period, and he has to hear himself to get it right. At times he sings sub-song, which consists of a near babble (very similar in concept to the babbling human infants exhibit during the language learning process). The male is comparing its voice to the song that was stored as a template during the sensitive period. Eventually, he develops a stereotyped song that is **crystallized** from this early “imprint”. Some species cannot change song after this point, whereas an **"open-ended" learner** species can change the song throughout life. The impact of a tutor's song is long lasting and plays a role in [deme recognition](#) through its effects on female choice for the songs that females heard as nestlings (father's song) (see Chapter 5).

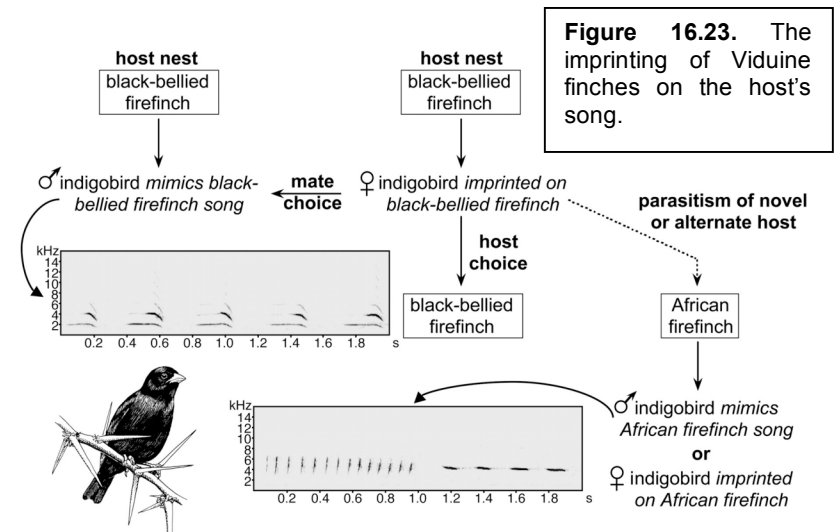
Another way to generate abnormal songs is to deprive them of contacts during the sensitive period. While such tutorless individuals do in fact develop a song it is typically highly abnormal relative to the species typical song. However, occasionally some song elements of the basic species song are preserved despite the absence of a tutor.

### Conservation and Plasticity of Song Across Seasons

The song production centers in most migratory songbirds regress every season as the levels of testosterone drop. Prior to the beginning of a new breeding season, the song nuclei begin growing again, and new circuits are born, and brand new neurons are recruited in the song centers (Nottebohm 1970, 1989). Recall [song recognition of neighbors](#) that Rene Godard (Chapter 7) demonstrated in a migratory species of birds. These birds can clearly remember a template of their neighbor's songs from the previous year. **Indeed, for such recognition to work, there must be some elements of a neighbor's song that remain static even in the face of such new neuronal growth.** In other species of birds (and whales), individuals in the local population change their song from year to year. In particular, less successful males model their song repertoire after the song repertoires of males that were successful the previous year (Eric Greene, pers. comm.). Such adaptive plasticity in song, clearly establishes that the song is not necessarily fixed after the song crystallizes in young birds. Such song plasticity could easily arise from the new circuits that are born with each new season.

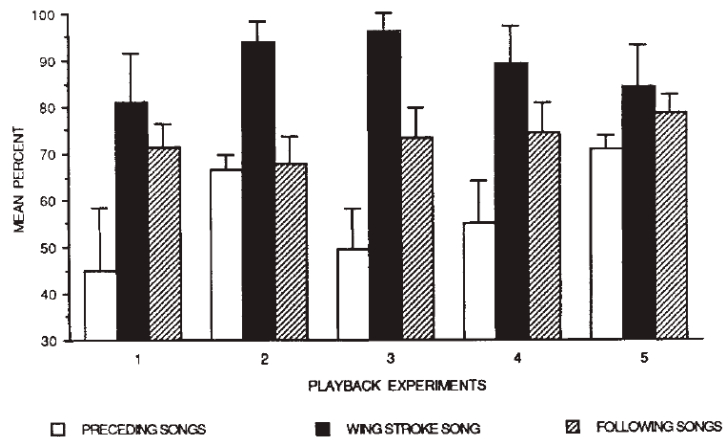
### Viduline finches and imprinting on host song

Consider the parasitic lifestyle of Viduline finches. These finches are born in a host-parent's nest, grow up and then learn a song during the sensitive period. Both male and female Viduline finches learn and imprint on host song. Later in life male Viduline finches sing the song of their host to impress females Viduline finches. Female Viduline finches prefer a male of their species that sings the song of their host-environment (e.g., neural template acquired during the sensitive period). Moreover, these females prefer to parasitize the nest of hosts that sing this song. This leads to demes of Viduline finches that learn a given hosts song, and they only interbreed with other Viduline finches that have likewise imprinted on the same host (in Fig. 6.24 these are black-bellied fire finches). As in Galápagos finches (Chapter 5), misimprinting might occur if the Viduline finches hear a neighboring African fire finch, thereby leading to a potentially new deme of Viduline finches that expands into an entirely new niche of as yet unexploited hosts. The coupling between host song in mate choice and host choice, can fuel a culturally selected runaway similar to a genetic Fisherian runaway process. This is a clear example, of **the environment external to the individual having a dramatic impact on neural circuits of an individual.** Such modification of neural circuitry points to routes by which novel behaviors might be acquired during an animal's lifetime.



## Tutorless Songs of Cowbirds

Cowbirds are also brood parasites that do not use classic song imprinting to learn the song of their host. Cowbirds appear to generate a template for song through an innate mechanism. The cowbird is a **brood parasite** that searches for hosts for her offspring. A cowbird host can be from an array of hundreds of different species unlike the precise matching of host species in Viduine finches. Most of the 200 potential host species of cowbirds have not learned to reject cowbird eggs or evolved an innate rejection mechanism that is necessary to skewer the egg and eject the parasite from their nests. Cowbird offspring are hatched by the unsuspecting host species. The cuckoo of Europe has a similar parasitic lifestyle and a few species have learned to reject the eggs deposited by the cuckoo, so it is not totally impossible for some kind of egg parasite recognition to take place. Given that the host birds rear the cowbird chick during the sensitive period for song, it must be the case that cowbirds have some kind of **innate template** for its own species-specific song.



**Figure 16.19.** The mean percent copulatory responses by eight females in each of five separate playback experiments. In each experiment the wing-stroke song received the highest rank in terms of copulatory response from females. These males were all untutored but had a female in the cage during their song-learning period (from West and King 1988).

When the cowbird matures it sings a species typical cowbird song, which is totally different from its host species. Meredith West and Andrew King (1988) isolated male cowbirds after they fledged from their hosts. They isolated the males from other male tutors, but they did provide each male with a female. Female cowbirds do not sing a note, thus, they thought that the female would not provide any feedback for the males song. Males that were isolated from other males, but not females, did not learn to sing the species typical song. Rather they sang an abnormal song. The loud whistle in the final phrase of the song, was the most divergent element (referred to as song 9 or the wing stroke song). It appeared that cowbirds needed a male tutor to learn the species-specific song. West and King then decided to assay the potency of the song of these males compared to males that had tutors, by playing the tutorless and tutored male songs to a group of receptive females. They were astonished to find that the tutorless songs were more potent in eliciting lordosis from the females compared to most of the tutored males' songs.

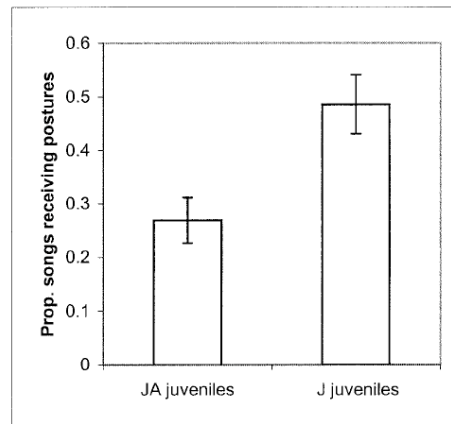
How could this be if the tutorless males only had the mute females as a companion that generated feedback? How could they learn a song without other experienced males to sing a template for them? Young male cowbirds do appear to have an innate template for the species-specific song. However, the template does need to be refined by interactions with both male and female conspecifics. They do not need to hear other males to develop a sexually potent song. They only need interactions from the non-singing females. Recall the [videos on non-song communication](#) between female and male cowbirds. We have already seen how females have a variety of gestures for communicating their lack of interest in copulation. West and King have found that females use a pointing gesture to give males more subtle visual feedback regarding his song. The male presumably modifies his newly developing song in direct response to such visual gestures.

This kind of communication is a classic example of the "**audience effect**". The un-tutored cowbird males had a captive audience in the form of a female. The female provided the males with visual cues during his song learning that allowed him to modify his song into a really potent song. Their tutorless songs were so potent that they outperformed the tutored song of most other birds in a flock. However,

tutorless songs were on par with the songs in terms of sexual potency as the songs produced by the most dominant males in a social flock.

How do such un-tutored males behave in a more complex social environment? Cowbirds are quite gregarious creatures and they do aggregate during their first winter. In such aggregations, a young cowbird could easily learn and refine his own song by using both the males and females around him as tutors. West and King have clear evidence of young males associating with females in such flocks preferentially. However, they do appear to interact with males. There are clear dominance hierarchies in such flocks. Dominant males are intolerant of males that sing a provocative song -- one that stimulates the female too much. The dominant birds punish tutorless birds for their lyrical acts of insolence.

For example, if West and King placed any of the tutorless males (those that sang potent songs) into aviaries with established dominance hierarchies, dominant birds attacked them on the first few notes. A male needs feedback from females, but he also needs feedback from other group members so that he learns his place in the dominance hierarchy of the flock. Once a young male establishes his dominance in the flock, he might be able to let loose a little and try out some of the more provocative song elements that are more stimulating to the females. Therefore the song of cowbirds is really a potent badge of status (see Chapter 8) that is acquired through long-term dominance interactions with other male members of the flock.



**Figure 16.20.** Juvenile males reared without (JA) and with a female (J). (from West and King 1988).

## Summary of IRMs, FAPs and Innate Behaviors

The view that I have developed in this chapter is that the interactions among organisms are virtually parallel in form to the interactions of sender and receiver molecules of development. These behavioral interactions generate a cascade of changes in the receivers that is akin to a genetic program. We can develop cellular automata programs of such behavior and generate the remarkably complex patterns of ant foraging with a simple set of programming steps.

The full series of gene interactions that lead to IRMs and FAPs will be uncovered in the next decade. In some systems the information is nearly complete. For example, the interactions in social insects are well characterized in terms of the signaling molecules (royal jelly), transcribed genes (insulin-like proteins), endocrine cascade (JH-ecdysone) and even the proteins that are expressed. The only information that is currently lacking is the genes in the nervous system that might undergo synaptic plasticity to alter short and long-term responses to conspecifics.

## Late Onset Brain Neural Development

### Classical Ideas on Development of the Nervous System

The classic paradigm underlying neuronal development in vertebrates is that neurons grow and proliferate during embryogenesis. In fact, many more neurons are produced than are found in the adult. Through a process of cell death, neurons that were not "connected" to other neurons would be removed from the system. Gerald Edelman (1987) came up with the idea of "Neural Darwinism" in which neurons compete to produce the "right connections" during early development. The actual behavior and motor control circuits reinforce the connections between nerves. Those that are participants in an "active circuit" would live, whereas those connections that are not participants, would die. In this way the nervous system of a vertebrate would be whittled down to a small subset of the possible to connections, to those connections that work. This simple view of development is purely epigenetic (above the genes).

Connections that work are those that survive, there is no real genetic code for the connections. It is now clear that many connections are indeed programmed by the interactions between gene products. Substances are laid down in the developing embryo that guides the development and growth of neurons such that the neuron correctly innervates the correct targets (e.g., sensory or motor neurons of the peripheral nervous system). It is also clear that such connections can be modified by social experience via synaptic plasticity (see the example on crayfish in Chapter 8).

formed in those mice in depauperate sensory environments. These experiments have now been repeated and the evidence reinforces the view that the adult brain is not a static set of neural circuits, but it may have the capacity to adapt to challenges from the external environment. The studies also show an interesting link between the complexity of the environment and complexity of connections in the brain. These connections are formed as the animal learns, which is the subject of the next Chapter (17).



Figure 17. 21. Enriched environments thicken the somatosensory cortex of the rat (from Diamond et al 1964).

For many years, it was thought that all of these events were restricted to early development, and there couldn't be much new neuronal birth after an animal matures. The case of song neural development in birds in which song nuclei grow and retreat with the seasons has provided a startling counter-example to this view.

Still others cling to the view that this was a special case and vertebrates did not have the capacity for further neuronal growth and proliferation after early development. *Neuronal Development in Adult Mice and Enriched Environments* Marian Diamond et al. (1964) began a series of experiments in the early late 60's that were to provide additional evidence for a more plastic nervous system in adults. She began rearing mice in a variety of environments that she classified on the basis of enriched or depauperate in sensory information. An enriched environment included a world filled with novel tactile cues, objects with strikingly different shapes (balls, squares, etc.), compared to environments that had none of these added stimuli. She found that a region of the brain, the hippocampus, showed pronounced increases in the number of new neurons compared to the brains of the mice at the start of the experiment. In contrast, no new neurons or connections were

### **Study Questions: Genes, Environment, Development and Behavior**

1. Explain how sign stimuli involved in species recognition trigger a reply from another individual. Your answer must include the proper terminology (e.g., innate releasers and FAP). To focus your answer, explain the process in terms of motion detection and signature displays of *Anolis* lizards (review the movies on species recognition in *Anolis*)
2. Could imprinting be considered a form of learning? Explain your answer in terms of associative theories of learning.
3. Explain caste determination in social hymenoptera. Be sure to explain where males (drone), queen, and sterile workers come from.
4. If an ant colony has no real leader, then how can the activities of the colony be coordinated?
5. All workers have the same morphology in a bee colony and yet workers are clearly specialized in various roles. What are four different roles or tasks that workers perform? Explain three competing theories that describe how tasks are allocated in a bee colony.
6. In contrast to bees, ants produce very different kinds of sterile workers. How does environmental control over caste determination in ants allow for a colony to be efficient in allocating workers to tasks?
7. Why does a cowbird have to have an innate sense of his species song? Even though his song is innate describe the effect of each sex on a cowbird male's developing song when he rejoins the flock of cowbirds during his puberty?
8. What is the advantage of a species typical song like that of a cowbird, compared to an imprinted song like that of a Viduine finch. What are the disadvantages of this form of song learning.