http://www.pbs.org/wgbh/nova/ants/queen.html

BEING QUEEN BY PETER TYSON

Dwarfing her attendant daughters, a queen leafcutter ant rests amidst the white fungus that her workers cultivate on leaf bits inside the nest. She can live 30 years.

Like their counterparts in human society, Nature's queens seem to have it all. They're pampered, fed, guarded, and don't have to lift a finger except to produce royal heirs. But being queen isn't all peaches and cream. Queens of all kinds of social animals—ants and termites, certain species of bees and wasps, and the sole social mammal, the naked mole rat—are under constant pressure to produce new generations and to hold onto their reproductively supreme positions.

MEETING HER EVERY NEED

On the face of it, queens appear to have it made from the get-go. Take the honeybee, *Apis mellifera*. Unlike the thousands of workers developing in nearby cells in the brood comb, a honeybee queen larva, chosen by the workers, lives in a more spacious cell and gets fed a nutritious, high-calorie diet called "royal jelly." This diet turns her into a fertile queen, and if she is fortunate enough to take over the colony, she goes on to monopolize reproduction. She becomes the only member of the entire colony that gets to mate and pass on her genes to the next generation.

This begins on her nuptial flight, during which a new queen honeybee mates repeatedly, amassing over 70 million sperm from multiple males. (For a male, it's the end of the line: During copulation, its endophallus breaks off inside the queen, rupturing its abdomen and killing it.) A single fertilization supplies a lifetime's worth of sperm, but by mating with several males the honeybee queen improves the genetic diversity of her offspring, enabling them to better withstand disease. Queen ants, for their part, settle for just a single sexual encounter, storing all the sperm they'll ever need in a special sac.

After she is fertilized, a queen settles into a life of procreation. In many cases she establishes her own nest, often alone but sometimes with other queens; in others, she assumes control in a nest already built, either by being raised in it or by hijacking it from another queen or settling into an orphaned colony. Once established as doyenne, all she has to do is generate eggs. Even in an emergency, she may not have to move a muscle—her entourage will carry her to a safe location.

To protect its queen, a soldier of the army ant *E. burchelli* will attack anything with its fearsome-looking mandibles.

GUARDED FOR LIFE

Indeed, a President would envy her level of protection. To safeguard their matriarch, honeybees, for instance, will form a tight cluster around her. Social species that, unlike the honeybee, don't have nests, offer even greater security. Workers of *Eciton burchelli*, a species of army ant, protect their queen by fashioning a living shelter out of their interlocked bodies. This elliptical mass may be three feet across and hold up to 700,000 ants. When they need to move to a new site, where they bivouac on the surface rather than build a nest, *E. burchelli* workers go first, ferrying food and larvae. Only after nightfall does the queen follow, escorted by a mass of soldier ants that completely surround her and will

defend her with their lives.

> In just a few days, a single army ant queen can lay up to 300,000 eggs.

In part because of such attention, but also for genetic reasons not fully understood, the queen in many species lives essentially forever—at least from the perspective of her descendants in the colony. Queens of the black garden ant, *Lasius niger*, for example, live for an astonishing 20 to 30 years. *L. niger* workers, which are all female, survive for one to three years, while the males last for only a few weeks. On a human scale under such terms, if an average man lived 70 years, an average woman would live about 2,500 years and an average queen perhaps 30,000 years.

All of this—the doting and the defending, the exclusive rights to mating and long life—enables queens to be right out front in the survival of the fittest. As long as the colony survives, and she survives as its queen, she will pass on her genes more effectively than any other member of the colony.

The queen black garden ant that will develop from this glistening larva could live 10 times longer than her doting workers.

A QUEEN'S RANSOM

Being queen does have its challenges, however, ranging from the simply taxing to the potentially lethal.

For many queens, the most hazardous time of their lives is when they set out as virgin queens to mate and to establish their own colony. The vast majority of virgin queen ants perish within hours of leaving their mother's nest, most destroyed by predators or parasites. Vulernability can even extend to queens safely couched within a nest. In colony collapse disorder, the term given to the recent mass disappearances of honeybees, the queen is often left almost entirely alone.

Queens that survive to successfully form their own colonies face new hurdles. For starters, they are expected to produce—and how. Honeybee queens deliver up to 2,500 eggs per day, and that's small potatoes for some queen mothers. In just a few days, a single army ant queen can lay up to 300,000 eggs.

In the honeybee, queens are bigger than workers, and their larger brood cells stand out from those of non-queens (above left). This allows for better "policing" of potential queens than in the Mexican stingless bee, whose queens and workers, and their brood cells, are the same size (above right, with queen larvae marked by an asterisk).

COMPETITIVE NATURE

If meeting the reproductive needs of an entire community weren't enough of a burden, queens, even in healthy colonies, are in a subtle struggle with their own workers, most or all of which are their own daughters. That's because, in the unconscious drive all creatures have to convey their DNA to the next generation, a queen and her daughters have different selective pressures. For queens, which are equally related to their daughters and sons, it's better to create new queens and males for them to mate with, in the hope of founding new colonies. But workers would prefer their mother to propagate a 3:1 ratio of females to males.

It all comes down to genetic relatedness. In social insects, females develop from fertilized eggs and have paired chromosomes—one from each parent—while males arise from unfertilized eggs and have single chromosomes—from the mother only. As such, female workers share up to 75 percent of their genes with their sisters, while they share only 50 percent with their mother (or even their own offspring, were they to have them) and just 25 percent with their brothers.

This is one of the leading theories, known as "inclusive fitness," as to why social insects became social in the first place: Females, which constitute the vast majority of a colony's members, benefit more from not mating and raising their mother's daughters, their sisters, than they would from mating and raising their own daughters.

Resembling a tiny walrus, the tusked, gerbil-sized naked mole rat, along with its hairy cousin the Damaraland mole rat, is the only mammal known to be "eusocial." That is, like ants and termites, it lives in a colony with castes (queens, workers, etc.) that share in raising young, which are often the offspring of a single queen.

ROYAL RIVALRY

Often a queen will have overt competition as well. Sometimes, for example, her own daughters will lay eggs of their own. In the wood ant *Formica truncorum*, for example, workers generate as much as a quarter of all eggs. In other species, queens must compete with other queens in the same colony. This competition can start very early. Healthy honeybee hives typically have just a single reigning queen. To help ensure this, a newly emerged queen will sting her sister queens to death as they clamber out of their brood cells, nipping in the bud any chance they will grow up and challenge her.

In honeybees, this queen-queen killing is kept to a minimum, because queens themselves are kept to a minimum. Larvae are reared in open cells, with queen larva cells distinctly larger than worker cells, so workers know, and can strictly control, which larvae will dine on royal jelly and develop as queens. As a result, only about 0.01 percent of honeybees become queens.

Stingless bees of the genus *Mellipona* have a different arrangement, and it can make life brutally short for many more would-be queens. Their larvae, both workers and queens, are reared in closed cells, with all the nutrients they need for development, and all cells are the same size. Workers can't tell which larvae are baby queens and which baby workers, with the result that—in the Mexican stingless bee, *Melipona beecheii*, for example—up to 20 percent hatch as queens. Because these surplus queens serve no useful purpose in the colony—they're not needed for reproduction and they can't work—they are decapitated or ripped apart soon after they emerge from their brood cells.

Worker termites tend to the massive, swollen body of their queen in this nest uncovered in the Okavango Delta of Botswana.

BULLYING FOR POSITION

In the end, regardless of advantages or disadvantages, being queen is all about having the best possible chance to pass on as many of one's own genes as possible. To help keep this coveted position, queens have diverse strategies at their disposal.

On strategy is simple authoritarianism. Consider that homeliest of mammals, the naked mole rat, which lives in underground colonies in arid regions of East Africa. Along with a hairy cousin, it is the only mammal known to form social colonies (in which, by definition, adults cooperate in raising the young, two or more generations overlap at the same time, and adults are divided into reproductive and non-reproductive "castes"—queens, soldiers, workers).

> One thing is clear—social colonies work.

For researchers, it's not clear how the naked mole rat queen manages to dominate other colony members. But they do know that the queen spends more time than other adult rats patrolling the colony's narrow tunnels. And when she meets another rat, she typically clambers right over it; all other members pass each other side to side. The queen also rams or shoves selected colony members nose to nose. In a study of a 40-member colony at the Chicago Zoo, the reigning queen not only did

the lion's share of the shoving, but she saved most of her aggression for the most fertile females—those who were itching to take her place and, if she were to die, would fight to the death to assume it.

QUEENS OF CHEMISTRY

Some queens use chemical means to keep workers in line. Queen bees, for example, can release a pheromone that appears to block workers' ability to associate specific smells with negative stimuli. This "brainwashing" pheromone, say the researchers who first detected it, may keep workers from realizing that hanging around their queen is unpleasant. The chemical might be the queen's insurance policy against any possible mutiny by younger workers.

Other matriarchs use chemicals to target a rival for intimidation. The tropical ant *Dinoponera quadriceps*, one of the world's largest ants at over an inch long not including antennae, has no queen per se but rather a single alpha female that rules for a year or two before being displaced. When she senses a rival in her midst, the alpha female may smear a chemical on her, after which a group of workers, likely her daughters, subdue the rival, sometimes immobilizing her for several days. Again, daughters gain the best selective advantage by prolonging their mother's reign, being more closely related to sisters than they would be to the offspring of any sister that took over as queen.

WHATEVER WORKS

It all comes down to what works, including in number of queens. Sometimes a single, egg-laying queen has a colony all to herself. Sometimes she has to share. (In their Pulitzer-winning book *The Ants*, Bert Hölldobler and E. O. Wilson describe a "supercolony" of 45,000 interconnected nests of an ant called *Formica yessensis* that reportedly contained over 1 million queens.) Often the number of queens varies within the same species. Rarely, there's even no queen.

Why the difference in queen number? How does the queen so greatly outlive all other members of the colony when she derives from the same genetic roots? How did social colonies come about in the first place? As recent discoveries show, scientists are busy trying to answer such questions, and are finding compelling answers.

One thing is clear—social colonies work. Social insects account for less than 2 percent of all insect species (the rest lead solitary lives). Yet their abundance and impact on ecosystems make them the dominant arthropods—insects, arachnids, crustaceans—in most land habitats. They are, as Wilson has so aptly put it, "the little creatures that run the world." And among those little creatures, one stands out like a living goddess—the queen. ■

Peter Tyson is editor in chief of NOVA online.

SELECTED SOURCES

Helanterä, Heikki and Liselotte Sundström. 2007. "Worker Reproduction in Formica Ants." The American Naturalist. 170: E14-E25.

Hölldobler, Bert and Edward O. Wilson. 1990. The Ants. Cambridge, MA:

Harvard University Press.

Jemielty, Stephanie, et al. 2005. "Long Live the Queen: Studying Aging in Social Insects." Age. 27:241-248.

Milius, Susan. 2006. "Naked and Not: Two Species of Mole Rats Run Complex Societies Underground." Science News. 24 June 2006. Vol. 169, No. 25.

Monnin, Thibaud, et al. 2002. "Pretender Punishment Induced by Chemical Signalling in a Queenless Ant." Nature. 5 September 2002. 419: 61-65.

Ratnieks, Francis L. W. and Tom Wenseleers. 2005. "Policing Insect Societies." Science. 7 January 2005. Vol. 307, No. 5706, pp. 54-56.

Seeley, Thomas D. and David R. Tarpy. 2007. "Queen Promiscuity Lowers Disease Within Honeybee Colonies." Proceedings of the Royal Society B: Biological Sciences. 7 January 2007. Vol. 274, No. 1606.

Vergoz, Vanina, Haley A. Schreurs, and Alison R. Mercer. 2007. "Queen Pheromone Blocks Aversive Learning in Young Worker Bees." Science. 20 July 2007. 317: 384-386.

Waldbauer, Gilbert. 2000. Millions of Monarchs, Bunches of Beetles: How Bugs Find Strength in Numbers. Cambridge, MA: Harvard University Press.