embryo. Thus, these physical arguments lend considerable credence to the view that elastic mechanical force, which travels at the speed of sound, is highly efficient at transmitting information rapidly across the spindle.

One aspect of the oscillations that remains unclear is whether they are really transverse in a single plane. What determines this plane of transverse oscillation? Alternatively, one might expect that, because of symmetry about the spindle axis, the oscillations might actually manifest themselves as a precession about the spindle axis, perhaps like a spinning top that precesses about its spinning axis. These more detailed three-dimensional aspects will provide further challenges to the model.

Nevertheless, Pecreaux *et al.* [7] have developed a relatively simple model that explains a variety of aspects of a very complex system. Is this the 'correct' mathematical model? One could always, in principle, posit alternatives that might also explain all the data at hand, and so there is never any 'unique' solution to the problem. Nevertheless, the hallmarks of a good model are that it holds up to repeated testing, that it makes surprising predictions that turn out to be true, and that it explains a lot with a little. The results of Pecreaux *et al.* [7] meet these subjective criteria, and provide both a relatively simple explanation for spindle movements in *C. elegans*, and a fundamental theoretical framework for further investigation of asymmetric cell division.

In summary, the antagonistic motor model has been subjected to a number of experimental tests, some of which would have been difficult to conceive without the modeling — the slight change of the oscillation frequency during build-up and die-down — and the same explanation emerges consistently: motor persistence builds monotonically during the first mitosis of *C. elegans.*

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# Social Evolution: Early Production of Deadly Males by Competing Queens

**Males usually have little involvement in the dramas of social insect societies, but a newly identified *Cardiocondyla* ant species has been found to produce long-lived, murderous males, even before the first workers, in a new form of queen–queen competition.**

**Joan E. Strassmann**

Understanding conflict and its resolution has been the goal of much social insect research ever since Hamilton taught us how to think about selection in groups of relatives [1,2]. Conflict arises in ant, bee and wasp societies because colony members are not genetically identical. Evolutionary strife can occur over sex ratios because workers and queens are not equally related to the next generation of males and females. [3–6]. For example, this difference in interests causes nearly complete specialization in male or female production in tropical wasp colonies [7]. Workers and queens may differ over who should produce males — virgin workers can produce males which are haploid. This conflict results in the methodical policing by honeybee workers on the lookout for rogue worker-laid eggs [2]. Interests can also differ over whether a given female should become a worker or a queen [2]. In *Melipona* stingless bees, many females become queens that are executed by the workers [8].

Workers are the most numerous party in colonies, and therefore often have the power to enforce their interests, but conflict need not involve workers [9]. Multiple-queen colonies are widespread in ants, bees and wasps, and competition between queens in the same colony is common [6,10]. For example, a newly emerged honeybee queen stings sister queens to death before they get a chance to challenge her [11]. Killing her competitors is important to a young queen because a honeybee colony can normally equip only one daughter queen with the workforce she needs after the original queen departs with a swarm of workers.

Queen conflict can also take more unusual forms. In this issue of *Current Biology* [12], an undescribed Malaysian species of *Cardiocondyla* ant is reported to exhibit a novel form of queen–queen conflict that results in extremely early male production. This competition to produce the first male is so intense that queens break one of the most basic of all social insect rules: produce workers before reproductives. Investing first in workers that defend and feed the next generation has long been considered an optimal strategy, critical to colony success [6,13]. So how do we explain the production of males, notorious for their lack of helping behavior, before the very first worker?

Not all colonies of *Cardiocondyla* sp. produce males precociously; queen number matters. To examine the impact of queen number on male production, Yamauchi *et al.* [12] set up two kinds of colonies, those with single queens, and those with two queens. Each new colony was also provided with a few workers and brood. Queens in the two-queen colonies produced males immediately, even before the first workers. The first-born male then killed all other developing males so he alone could mate in the nest with the future queens that emerge much later, after generations of workers. By contrast, in single-queen colonies, the queen produced males eight weeks later than two queen colonies did, only shortly before new queens emerged. This suggests there is a cost to precocious male production.

It turns out that precocious male production in *Cardiocondyla* sp. is the natural result of its life history, and a striking confirmation of predictions from social evolution theory. The costs of early male production are diminished because colonies never go through a single-queen stage. Instead new colonies are formed from segments of their natal colonies. A few workers carrying brood and one or more queens walk to a new nest site, under bark of trees in the Malaysian rain forest. This is quite different from most ant genera where colonies are begun by a single queen who has mated away from the nest and then found a safe nest site alone [6]. There she rears the first precious workers by feeding them her own eggs.

Because new colonies of *Cardiocondyla* sp. are founded by budding, it makes evolutionary sense for queens to mate within their colonies, thus avoiding the risks of predation while flying to and from a mating site. It is this inbred mating preference that is likely to be driving the whole system. Because queens mate at home, there is no general competition for their favors, as is the case in the majority of ant species that have mating flights. If the young *Cardiocondyla* queens come from a colony with a single queen, then they mate with their brothers. This sets up a condition known as local mate competition, something that favors production of only enough males to inseminate the available females [4,14,15]. This is because, from the mother queen's point of view, additional males are useless as they just take matings away from each other and all sons are equally related to their mother. The queen is in charge of male production, because *Cardiocondyla* workers do not possess ovaries, another condition unusual in ants.

If, however, the colony has multiple queens, selection will cause queens to behave in ways that increase her chance of producing the successful males in competition with other queens. These males then fight for mating rights. In *Cardiocondyla*, male–male battles have selected for males with weapons seldom found in ants [16,17]. In the species studied by Yamauchi *et al.* [12], males have saber-toothed mandibles that allow them to immobilize and kill other males. Males also smear their rivals with hindgut secretions, something that causes workers to kill the defiled males [12,18]. As a rule, older males kill younger males, sometimes before they have fully matured.

Because the oldest male kills all subsequent males, only the queen that produces the earliest formicidal male will pass on genes through the male line. This puts the queens into an arms race to produce males earlier and earlier. Males produced even before the first workers can only be successful because of a pair of other adaptations: long life and extended sperm production that continues throughout life. Yamauchi *et al.* [12] found that the males produced in multiple-queen colonies lived an average of 210 days, long enough to mate with the much later emerging queens. This makes them the longest-lived male ants known [12]. Phenomenal male longevity and a reduction in senescence probably evolved in ants more easily than in solitary insects because queens have already been selected for longevity [19]. This long male life is only useful because males can produce sperm throughout their life. Most adult male ants have degenerate testes and cannot renew their supply of sperm [20].

Almost 35 years ago, the firefly biologist, James Lloyd, recommended that I get to know an obscure insect genus well, then answer the theoretical questions it posed. *Cardiocondyla* would have been a good choice. *Cardiocondyla* sp. and its unusual form of queen competition provide a beautiful case study of the force of competition even in highly cooperative social insects. Inbreeding and colony budding avoid the hazardous single-queen stage of most ant life cycles and play out as a remarkable set of adaptations: exceptional male longevity, extended sperm production, lethal male battles, novel weapons for those battles and a backwards colony cycle when queens compete.

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# Cellular Biophysics: Bacterial Endospore, Membranes and Random Fluctuation

**Purposeful motion of biological processes can be driven by Brownian motion of macromolecular complexes with one-sided binding biasing movement in one direction: a Brownian ratchet, now proposed to explain membrane motion during a phagocytosis-like process in bacteria.**

**Vladimir Lizunov**
**and Joshua Zimmerberg**

In 1905, Albert Einstein published his papers on Brownian motion and put the last nail in the coffin of arguments against the kinetic-molecular view of matter. Molecules are subject to random fluctuations and undergo eternal motion. He showed how random fluctuations in molecules give rise to seemingly purposeful motion, as in the unidirectional flux that arises from diffusion down a gradient (summarized in [1]). Fifty years later, in 1957, Andew Huxley [2] proposed that thermal fluctuations can give rise to directed motion of biological motors. It was not until the 1990s that theoretical studies by pioneers Fumio Oosawa and George Oster were coupled to biological experimentation by Ron Vale and Sandy Simon, respectively, to develop models involving thermal or Brownian ratchets to explain either mechanisms of mechanochemical transduction of energy or translocation of proteins across membranes [3,4].

Although the second law of thermodynamics prohibits the production of heat or work from thermal fluctuations, this only holds true in equilibrium. Biological systems are far from thermodynamic equilibrium — equilibrium is synonymous with death, not life. So the gedanken experiments of Maxwell's demon and the Feynman ratchet [5] are gaining increasing attention in biology. A deterministic motor moves because of direct forces applied in the direction of movement, while a Brownian motor uses a chemical reaction to prevent backward displacement, thereby rectifying thermal fluctuations into unidirectional motion [6]. But fluctuations alone cannot do the work: asymmetry is the hidden energy storage, as for example in a concentration gradient or asymmetric potential profile. Asymmetry, or bias, can either exist prior to any interactions, as in rectifying channels for example, or it can be created during ratcheting, as for example in the distinct ATP-bound *versus* ADP-bound conformations of motor proteins [7,8].

Now, Brownian ratchets have been proposed as the mechanism of membrane motion during endospore formation in bacteria [9]. While, to most people, bacterial endospores are associated with the dreaded *Bacillus anthracis* and *Clostridium* species *tetani*, *botulinum* and *perfringens*, there is a universe of fascinating processes that occur during sporulation that can shed light on similar eukaryotic processes, such as development, membrane remodeling, phagocytosis and, now, the biophysics of membrane motion. Endospores are dormant cells specialized to allow a bacterium to survive adverse environments for long periods, but to return to the usual 'vegetative' state when favorable conditions are restored. Produced by members of the Firmicute family, they are resistant to many of the agents we use to kill bacteria, such as lysozyme, boiling, drying, radiation and disinfectants, such as alcohol and quarternary ammonium compounds (it is a good thing that *Eschericia coli* does not make