

Cockroach-termite evolution

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Cockroaches and termites, both classified under the order Blattodea with termites having evolved from cockroach ancestors, occupy the role of keystone species in ecosystems. Cockroaches are efficient recyclers of organic matter, while termites are powerful decomposers of wood and environmental engineers. Together, they ensure the smooth flow of energy and

material cycles, creating living conditions for countless other organisms. Their ecological role depends deeply on the social evolution, prompting questions about the mechanisms of natural selection. For instance, Darwin's principle of "survival of the fittest" struggled to explain altruistic behaviors, such as worker bee sterility or warning kin-that reduce or eliminate an individual's

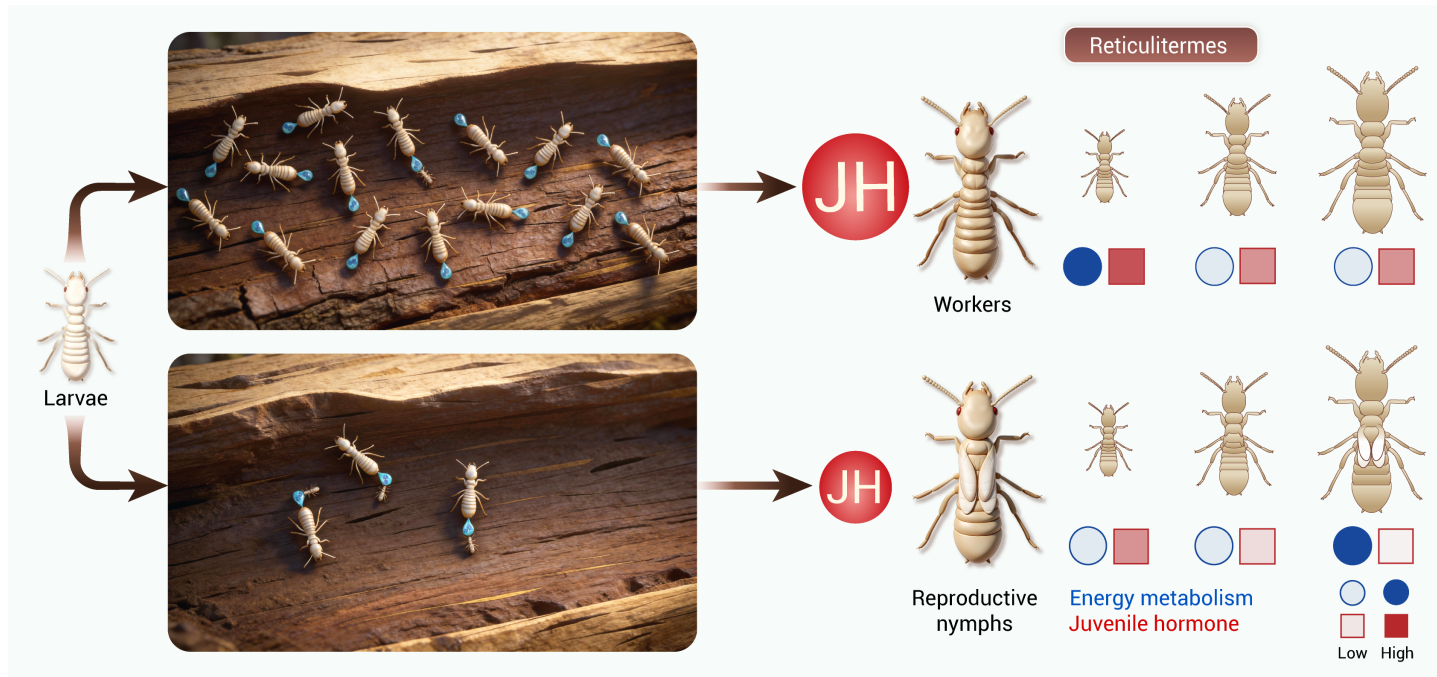


Figure 1. Differential nutritional allocation by sibling workers for caste differentiation in termites High provisioning elevated JH titers, leading to worker formation and sterility, whereas low provisioning with reduced JH titers resulted in reproductive nymphs. The increased activity of nutrition-sensitive pathways in larvae further promoted worker differentiation. These results demonstrate that differential nutritional allocation regulates the reproductive division of labor in termites.

own reproduction. Such traits should be eliminated by individual-level selection, yet they persist. This paradox was resolved by W. D. Hamilton (1964)^{1,2} who argued that the assessment of whether a trait is "adaptive" should not rely solely on the direct offspring count of the individual bearing it, but on its total effect on propagating all copies of the underlying genes, in both self and relatives. Thus, gene preservation and transmission form evolution's fundamental driver—a theory (later termed as the Hamilton's rule) supported by studies of ants, social bees, and ancestral monogamy in wasps.^{3,4}

Compared to the social origins in holometabolous groups like Hymenoptera (ants, bees, parasitoid wasps, etc.), the origin of sociality within Blattodea is more ancient. However, significant variation in habitat, diet, morphology, behavior, and physiology among Blattodea makes studying social evolution particularly challenging. Blattodea encompasses non-social, omnivorous cockroaches, dead-wood feeding cockroaches with biparental care, and termites with sibling altruism. Woodroaches occupy a narrow niche in mid-to-high latitude or high-altitude regions with low to moderate ambient temperatures. They are typically larger, develop slowly, and maintain small family groups of fewer than 20 individuals. In their cold habitats, they have lost energetically costly wings, and mitigate nutritional constraints through trophallaxis, where parents feed hindgut fluids to their offspring. However, termites differ markedly: they inhabit warmer environments, are smaller, develop rapidly and exhibit distinct social division and caste differentiation. Generally, a colony contains a large king and queen, with the queen producing numerous offspring. These are nourished by older siblings via trophallaxis. As

larvae mature, they differentiate into workers caring for siblings or into reproductive nymphs, based on colony needs. Workers can further differentiate into soldiers for defense. Wood-dwelling termites with one-piece nesting show limited conditional altruism, seen in false workers and some soldiers, whereas foraging termites have evolved unconditionally altruistic true workers.

Importantly, the origin of sociality within Blattodea coincided with the dietary shift from omnivory to dead-wood feeding. What were the driving factors in the formation of sociality during this evolutionary process? How can Hamilton's rule explain the altruistic behaviors observed in the varying degrees of sociality within Blattodea, and what are the underlying genetic mechanisms? In this commentary, we describe findings from a recent study published in *Science* by Cui et al. that reveals how nutritional specialization drove the emergence of distinct social behavioral strategies and elucidates the genetic mechanisms underlying termite caste differentiation, providing a novel framework for understanding the formation of insect social behaviors (Figure 1).⁵

The researchers obtained high-quality genomes of three cockroach species, one wood-feeding cockroach with biparental care, and four species of termites with sibling altruism. They found that social evolution in Blattodea is associated with genome contraction, not expansion. Termite genomes are significantly smaller than those of cockroaches, with the woodroach genome size being intermediate. This reduction correlates with a substantial loss of genes and a contraction of gene families, particularly those involved in metabolism, detoxification, and sensory functions. These

findings indicate that the contraction of the genome is an adaptation to environmental changes, and that adaptive innovations in social Blattodea are driven not by transcription of novel genes but by novel combinations of gene expression. Crucially, termites uniquely lost a suite of genes critical for sperm flagella motility, which are retained in promiscuous cockroaches and the woodroach. The most basal termite, *Mastotermes darwiniensis*, retains some of these genes and produces feeble, multi-flagellated sperm, while all other studied termites produce sperm that lack flagella completely. This suggests an absence of sperm competition within the termite female reproductive system, providing important evidence for the emergence of monogamy as a prerequisite for the evolution of reproductive altruism, as explained by the Hamilton's rule.

Next, the researchers revealed through transcriptomic analysis across developmental stages how energy metabolism underpins growth rate differences. Slowly developing woodroaches showed consistently low expression of oxidative phosphorylation and peroxisome genes, which are key pathways for energy metabolism. In contrast, rapidly developing cockroaches and termites exhibited high expression of these genes. Within termites, which has a bifurcated caste differentiation, the expression profiles diverged: early-stage workers showed peaks in energy metabolism gene expression, while late-stage reproductive nymphs showed a later, stronger peak. This indicates that caste differentiation is associated with differential allocation of nutritional resources and energy investment during development in the termite colony.

The study further elucidated the evolutionary adjustment of juvenile hormone (JH) signaling. JH titers decreased during development in cockroaches but remained constant in the slow-growing woodroach. In *Reticulitermes*, JH titers were high in early workers but an order of magnitude lower in reproductive nymphs. Experimental treatment with a JH mimic (methoprene) strongly induced the expression of *Kr-h1* in reproductive nymphs but had a minimal effect on workers, demonstrating that the two castes have evolved differential sensitivity to JH. This differential sensitivity, high in nymphs and low in workers, represents a key evolutionary innovation that "canalizes" development into distinct castes based on nutritional input. This divergence implies that JH might promote a foraging, non-reproductive trajectory in workers while permit reproductive nymphs to develop with low JH, enabling eventual metamorphosis into alates.

The following investigation into nutrition-sensitive signaling pathways (Insulin/IGF, EGFR, TORC1) showed that their activity, along with downstream Dpp signaling, peaked in the fat bodies of early workers and late reproductive nymphs of *Reticulitermes*. This pattern correlates with high energy metabolism in these stages. Inhibition of these pathways in early workers shifted their global gene expression profile to resemble that of early reproductive nymphs. Conversely, JH treatment of early reproductive nymphs shifted their transcriptome towards a worker-like profile. These experiments functionally link nutrition sensing, JH signaling, and caste-specific gene expression.

Furthermore, the researchers explicitly demonstrated that caste differentiation is regulated by sibling provisioning. In *Reticulitermes*, varying the ratio of nursing workers to larvae directly influenced caste outcomes: high provisioning rates (more nurses per larva) led to almost exclusively worker development, while low rates allowed some larvae to develop into reproductive

nymphs. High provisioning correlated with elevated JH titers and increased activity of nutrition-sensitive pathways in larval fat bodies, channeling development towards the worker trajectory (Figure 1). For the first time, this experiment provides strong evidence that nutritional sensing regulates JH signaling to control reproductive division of labor.

Based on the above findings, the researchers further proposed an evolutionary model for Blattodea sociality: (1) Wood-feeding cockroaches, despite exhibiting gregarious behavior and biparental care, do not evolve sibling provisioning and nursing due to parental promiscuity, which is insufficient to promote altruism; (2) OP nesting wood-dwelling termites maintain strict monogamy only initially. As offspring later prioritize reproduction, kinship declines, leading to conditional altruism, manifested as false workers; (3) Foraging termites practice strict lifelong monogamy, sustaining high kinship and enabling unconditional altruism via sterile true workers.

In conclusion, this research integrated genomics, transcriptomics, and more importantly, functional verification, to reveal a coherent evolutionary narrative. The transition to sociality in termites involved substantial genomic streamlining, the loss of traits linked to sexual competition, and the co-option of conserved developmental and metabolic pathways. The evolution of obligate altruism required not only high genetic relatedness (from strict monogamy) but also a mechanistic coupling where nutritional provisioning by siblings modulates JH signaling and energy metabolism, directing individuals into distinct, adaptive developmental castes. This research on the adaptive evolutionary mechanisms of social insects is not only a core topic in entomology or evolutionary biology but also provides critical insights for ecology, genetics, and behavioral science. More fundamentally, it offers a mechanistic blueprint for how environmental cues (such as nutrition) are translated, through conserved signaling pathways, into complex social phenotypes. The survival strategies developed by these "tiny engineers" through hundreds of millions of years of evolution serve as an invaluable knowledge base for humanity to understand the complexity of nature and address future challenges.

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AUTHOR CONTRIBUTIONS

All author contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The author declares no competing interests.