AN-07 Social insects and extreme reproductive division

Introduction: The Apex of Reproductive Division

Eusociality represents one of the major evolutionary transitions in biological history, characterising the pinnacle of reproductive division of labour. The defining features of eusociality include overlapping generations, cooperative brood care, and a strict division of labour into reproductive and non-reproductive castes[1]. In the Hymenoptera (ants, bees, and wasps) and the Blattodea (termites), this phenomenon manifests in societies where the vast majority of individuals completely forego direct reproduction to raise the offspring of a single or few reproductive individuals.

In these societies, the concepts of "sex" and "role" diverge radically from mammalian norms. In the social Hymenoptera, societies are fundamentally female-centric, driven by a haplodiploid sex-determination system. Fertilised (diploid) eggs develop into females, which can become either reproductive queens or sterile workers, while unfertilised (haploid) eggs develop into males. Consequently, the worker caste—which undertakes all domestic, foraging, and defensive tasks—is exclusively female. The male caste (drones) exists solely as a fleeting vessel for gamete delivery; they perform no work, do not participate in colony defence, and typically die upon mating or at the onset of winter[3]. Termites, by contrast, are diplodiploid and maintain a worker caste comprised of both sexes, though they share the extreme reproductive skew seen in Hymenoptera[5].

Because eusocial insect colonies are capable of extraordinary feats of engineering, agriculture, and coordinated defence, observers frequently draw direct analogies between the "hive" and human society. However, applying the hive or "queen" metaphor to human families, organisations, or societies is biologically and sociologically misleading. A honeybee queen is not a political monarch exerting executive control; she is a captive reproductive ovary, entirely dependent on the collective decisions of her sterile daughters. Furthermore, human societies are rooted in the cooperative breeding and biparental investment of genetically distinct, diploid individuals. In human evolutionary history, both males and females provide critical, complementary caloric and developmental investments to highly altricial young over extended juvenile periods, fundamentally altering human life history (Kaplan et al., 2000, *Evolutionary Anthropology*)[6]. To conflate the kin-selected, female-only worker castes of haplodiploid insects with human social roles is to commit a profound naturalistic fallacy.

Nevertheless, while the reproductive structures of social insects offer no template for human gender relations or family structure, their mechanisms of conflict resolution, task allocation, and collective decision-making provide profound insights into the mathematics of cooperation, the mitigation of free-riders, and the emergence of group-level intelligence.

Layer 1: Physiology (Measurable)

The physiological layer of eusociality encompasses the genetic architecture of relatedness and the molecular and epigenetic mechanisms that translate a single genome into radically

divergent morphological castes.

The Genetics of Inclusive Fitness and the Monogamy Hypothesis

The physiological bedrock of hymenopteran eusociality was famously articulated by William D. Hamilton in 1964 (*Journal of Theoretical Biology*), who proposed that haplodiploidy predisposes the Hymenoptera to eusociality due to relatedness asymmetries[3]. Hamilton's rule mathematically dictates that an altruistic trait will spread if $rb > c$, where r is the genetic relatedness between actor and recipient, b is the reproductive benefit to the recipient, and c is the reproductive cost to the actor[4]. In a haplodiploid system, females share 50% of their genes with their mother and daughters, but because the haploid father passes on his entire genome, females share 75% of their genes with their full sisters.

Relationship (Haplodiploid)	Average Genetic Relatedness (r)
Mother to Daughter	0.50
Sister to Full Sister	0.75
Sister to Half-Sister (Polyandry)	0.25
Sister to Brother	0.25
Sister to Own Son	0.50
Sister to Nephew (Sister's Son)	0.375

Hamilton argued that because females are more closely related to their full sisters ($r = 0.75$) than to their own potential offspring ($r = 0.50$), natural selection strongly favours workers rearing sisters over reproducing independently[3]. However, this "haplodiploidy hypothesis" faced a mathematical crisis. If a queen mates with multiple males (polyandry), the average relatedness among workers drops to 0.25 for half-sisters. Furthermore, females are related to their brothers by only $r = 0.25$, which perfectly cancels out the 0.75 relatedness to sisters if the colony sex ratio is equal[3].

This paradox was definitively resolved by the "Monogamy Hypothesis," which underwent a rigorous phylogenetic test by Hughes, Oldroyd, Beekman, and Ratnieks (2008, *Science*). Examining female mating frequencies across 267 species of eusocial bees, wasps, and ants, Hughes et al. demonstrated that mating with a single male (monandry) is the ancestral state for

all eight independent origins of eusociality in their dataset[10]. The effect size was absolute: polyandry (>2 effective mates) is exclusively a derived trait, occurring only in lineages where workers have already lost reproductive totipotency[10].

Boomsma (2009, *Philosophical Transactions of the Royal Society B*) formalized this into the "monogamy window." When a female mates strictly once for life, workers are equally related to their own offspring ($r = 0.5$) and their full siblings ($r = 0.5$). Consequently, relatedness mathematically cancels out of Hamilton's equation[8]. This implies that any infinitesimally small efficiency benefit ($b/c > 1$) in helping rear siblings at a fortified maternal nest over risky independent founding will tip the evolutionary scale toward obligate eusociality. The physiological prerequisite for the evolution of extreme reproductive division is not genetic diversity, but strict, lifetime monogamy[8].

Epigenetics and Caste Determination: The Royalactin Controversy

Given that queens and workers share identical genomes, how does physiology dictate morphological fate? The divergence is entirely environmental, driven by nutritional inputs that trigger epigenetic reprogramming[13].

In a landmark study, Kucharski, Maleszka, Foret, and Maleszka (2008, *Science*) demonstrated that DNA methylation acts as the physiological switch for caste determination in the honeybee (*Apis mellifera*). Using RNA interference (RNAi) to knock down the expression of *Dnmt3* (DNA methyltransferase 3) in newly hatched larvae, researchers prevented *de novo* DNA methylation. The effect was staggering: 72% of the *Dnmt3* knock-down individuals emerged with the fully developed ovaries and morphology of queens, despite being fed a worker diet[13]. This finding replicated the effects of royal jelly, proving that the worker phenotype is an actively maintained, epigenetically repressed state, whereas the queen phenotype is the default trajectory when methylation is inhibited[13].

The precise nutritional trigger in royal jelly that lifts this repression remains the subject of intense controversy. Kamakura (2011, *Nature*) claimed to have isolated a 57-kDa protein, major royal jelly protein 1 (MRJP1), dubbed "Royalactin." Kamakura reported that feeding Royalactin to honeybee larvae—and notably to *Drosophila* fruit flies—activated the epidermal growth factor receptor (EGFR) pathway, resulting in larger body sizes, faster development, and ovary maturation, essentially synthesizing a queen[16].

However, this finding suffered a catastrophic replication failure. Buttstedt, Ihling, Pietzsch, and Moritz (2016, *Nature*) attempted a rigorous replication using identical protocols and found that Royalactin had absolutely no effect on queen determination, concluding that "Royalactin is not a royal making of a queen"[18]. Leading critics of the Royalactin hypothesis argue that caste determination is not driven by a single "magic bullet" protein. Instead, recent evidence points to a combination of diet quantity and inhibitory plant compounds. Lawson et al. (2020, *Proceedings of the Royal Society B*) demonstrated that larvae fed an *ad libitum* quantity of diet invariably developed queen traits, independent of specific protein-to-carbohydrate ratios, explaining 64.4% of the variance between castes[20]. Concurrently, Zhu et al. (2017, *PLOS Genetics*) identified that plant microRNAs found in "worker jelly" (which includes pollen and

beebread) actively delay development and inhibit ovary growth, effectively suppressing queen emergence[21].

Chemical Signalling: QMP and the Dufour's Gland

Colony physiology is coordinated through highly complex pheromonal networks. The Queen Mandibular Pheromone (QMP)—a blend of semi-volatile carboxylic acids including 9-ODA and 9-HDA—was historically viewed as a coercive agent that chemically sterilised workers against their evolutionary interests[22].

Modern interpretations, however, view QMP as an honest signal of queen fertility. When QMP is present, workers are physiologically inhibited from activating their ovaries because rearing the queen's offspring is mathematically more viable than attempting independent reproduction[22].

There is significant redundancy in this chemical architecture. Research shows that even if a queen's mandibular glands are surgically removed, her cuticular hydrocarbons and secretions from the Dufour's gland (specifically complex esters) continue to suppress worker ovary development and elicit retinue behaviour[22]. The occurrence of queen-like esters reliably signals fertility and dominance, proving that colony cohesion relies on a distributed matrix of chemical cues rather than a single glandular override[24].

Layer 2: Behaviour (Statistical, Overlapping Distributions)

The behavioural layer translates physiological predispositions into statistical, colony-wide phenomena. Individual insects display immense variability in their response thresholds, meaning behavioural patterns are best understood as overlapping distributions rather than rigid, robotic algorithms.

Conflict, Coercion, and Worker Policing

Despite the harmonious appearance of the hive, the colony is a hotbed of latent genetic conflict. In many hymenopteran species, workers lack the ability to mate but retain functional ovaries capable of laying unfertilised (haploid) male eggs. Because a worker is more closely related to her own son ($r = 0.5$) than to the queen's son (her brother, $r = 0.25$), a strong genetic incentive exists for workers to selfishly lay their own eggs[25]. If unchecked, this leads to a "tragedy of the commons," where too many workers reproduce, colony efficiency plummets, and the collective perishes[26].

This conflict is resolved through "worker policing," a behaviour formally defined by Ratnieks and Visscher (1989, *Nature*). In *Apis mellifera*, workers actively patrol the brood comb. If they detect an egg lacking the queen's specific chemical signature, they consume it (oophagy). The policing is ruthlessly effective.

Egg Source	Setting	Survival After 1 Hour	Survival After 24 Hours	Survival After 48 Hours
Queen-laid	Discriminator	~100%	65-70%	30-35%

	Colony			(natural attrition)
Worker-laid	Discriminator Colony	~5-10%	0-4%	0%

Data synthesized from Ratnieks & Visscher (1989) and related behavioural assays[27].
While approximately 7% of all male eggs are laid by workers, only 0.12% of adult drones are workers' sons, demonstrating near-total suppression of worker reproduction[25].
Wenseleers and Ratnieks (2006, *Nature*; 2006, *The American Naturalist*) conducted a definitive comparative analysis across 90 species of ants, bees, and wasps to test the evolutionary drivers of worker policing. They proved that worker policing occurs significantly more frequently in species where queens mate multiply. When a queen is polyandrous, workers are related to the queen's sons (brothers) by $r = 0.25$, but they are related to other workers' sons (half-nephews) by only $r = 0.125$ [25]. Therefore, the collective worker force has a genetic incentive to eat each other's eggs and rear the queen's sons instead.
Wenseleers and Ratnieks (2006) established the principle of "enforced altruism." Their data showed an inverse relationship between the effectiveness of policing and the rate of worker reproduction. Where policing is highly effective, workers evolutionarily "acquiesce" and do not activate their ovaries, as the cost of laying an egg that will inevitably be eaten outweighs the benefits[31]. Altruism in the hive is thus not entirely voluntary; it is enforced by a coercive policing system that aligns individual incentives with the collective good[32].

Task Allocation and Age Polyethism

The division of labour among sterile workers relies on statistical probability rather than strict dictation. This is achieved through "Age Polyethism" and the "Response Threshold Model" (Bonabeau et al., 1996; Theraulaz et al., 1998)[34].
Workers generally perform safe, interior tasks (nursing, cleaning) when young, and transition to dangerous, exterior tasks (foraging, defence) as they age[37]. However, this is not a rigid timetable. The Response Threshold Model posits that every worker has an internal, neurological threshold for a specific stimulus (e.g., the smell of hungry larvae, the accumulation of debris). If the stimulus exceeds the threshold, the worker performs the task, which subsequently lowers the stimulus in the environment, turning off the behaviour[35].
These thresholds are heterogeneous and shift with age and experience. When distinguishing what is known about averages from what can be said about individuals, we see immense individual variance. On average, age dictates role, but individually, a young bee may become a precocious forager if the colony's foraging force is depleted, driven by her specific response threshold[39]. Furthermore, not all workers are industrious. Dornhaus (2008, *PLOS Biology*) documented the phenomenon of "inactive" or "lazy" workers in *Temnothorax* ants. A significant

portion of the colony's workforce remains inactive for long periods. This inactivity is not a defect but an adaptive buffer, allowing the colony to rapidly scale its workforce in response to sudden ecological windfalls or structural damage, proving that optimal colony efficiency requires overlapping distributions of specialists and idle reserves[40].

Layer 3: Culture (Variable) and Collective Decision-Making

While social insects do not possess "culture" in the human sense of transmitted symbolic traditions, they possess a highly variable, structurally engineered environment and robust mechanisms for collective decision-making. The most exhaustively documented example of this is nest-site selection during swarming, a process Thomas Seeley (2011, *Honeybee Democracy*) famously compared to a democratic town hall[43].

Swarm Democracy and Quorum Sensing

When an *Apis mellifera* colony outgrows its cavity, the mother queen and approximately 10,000 workers swarm, clustering on a nearby branch[43]. Several hundred older foragers transition into "scout bees" to explore the surrounding landscape for a new home.

Through extensive experiments on Appledore Island, Seeley and colleagues quantified the highly specific criteria bees use to evaluate real estate: a cavity volume of roughly 40 litres, an entrance at least 5 metres off the ground, a small entrance hole (for defensibility), and southerly exposure[44]. Scouts evaluate cavities and return to the swarm to perform the "waggle dance," recruiting other scouts to their discovery. The intensity and duration of the dance (specifically the number of waggle-runs per dance) directly correlate to the quality of the site[46]. The swarm evaluates multiple options (often 12 to 24) simultaneously in a decentralised information market[47]. The process does not rely on a unanimous consensus, but rather a "quorum threshold." Seeley and Visscher (2004, *Behavioral Ecology and Sociobiology*) discovered that once approximately 15 scout bees are present simultaneously at a potential site, they sense the quorum[47]. The scouts then return to the cluster and produce a high-frequency "piping signal" (a 200 Hz vibration lasting 0.8 seconds) that prompts the resting bees to warm their flight muscles to 35°C[47]. In field trials presenting swarms with five nest boxes of varying quality (only one being ideal), swarms selected the optimal site with 80% accuracy[44].

Cross-Inhibition: The Stop Signal

An information market is vulnerable to positive feedback loops that could result in deadlocks if two sites are of equal quality. To resolve this, honeybees employ cross-inhibition via a "stop signal."

Seeley et al. (2012, *Science*) revealed that scouts advocating for one site will seek out dancers advocating for a competing site and deliver a brief, 150-millisecond vibratory signal at 350 Hz, usually accompanied by a head-butt[47]. This stop signal inhibits the recipient from dancing.

Decision Phase	Mechanism	Function	Outcome

Exploration	Independent Evaluation	Scouts assess sites without prior bias.	Prevents cascading errors based on poor initial finds.
Advertisement	Waggle Dance	Signal duration scales with site quality.	High-quality sites accumulate scouts faster.
Cross-Inhibition	Stop Signal (150ms, 350Hz)	Scouts suppress competing dancers.	Breaks deadlocks between equal-quality sites; suppresses inferior options.
Commitment	Quorum Threshold (~15 bees)	Triggers Piping Signal (0.8s, 200Hz).	Warms flight muscles; terminates debate for lift-off.

The stop signal scales with the quality of the site and the accumulation of scouts, operating identically to the mutually inhibitory neural circuits found in the primate brain during decision-making[47]. At the individual level, coding is noisy—the "discoverer-should-dance" phenomenon means the first bee to find a site will likely dance for it regardless of its absolute quality[52]. However, at the average, population level, individual errors are filtered out through decentralized verification and competitive cross-inhibition, yielding highly accurate collective choices from highly flawed individual inputs[52].

The Kin Selection vs. Group Selection Controversy

The theoretical foundation of the social insect literature—kin selection and Hamilton's Rule—recently became the subject of one of the most intense and publicised academic conflicts in modern evolutionary biology.

In 2010, Martin Nowak, Corina Tarnita, and E.O. Wilson published "The Evolution of Eusociality" in *Nature*, arguing that inclusive fitness theory was mathematically limited, required overly stringent assumptions, and was fundamentally inferior to standard population genetics[53]. They argued that relatedness was a consequence, rather than a cause, of eusociality, and that ecological group selection alone was sufficient to explain the evolution of the hive[53]. Nowak et al. boldly claimed that Hamilton's rule "almost never holds"[56].

The response from the biological community was unprecedented. Abbot et al. (2011, *Nature*) published a rebuttal co-signed by 137 evolutionary biologists, outright rejecting Nowak et al.'s premise[57]. The leading critics, including Andrew Bourke, J.J. Boomsma, and Andy Gardner, pointed out that Nowak et al. relied on an unrealistic mathematical model that treated workers

as mere genetic extensions of the queen, ignoring the vast empirical reality of worker-queen conflict and worker policing[55].

Subsequent mathematical analyses tested Nowak et al.'s model against Hamilton's rule. Liao et al. (2015, *PLOS Biology*) found that when workers' genes are allowed to independently influence their own behaviour—rather than being treated as robotic appendages of the queen—eusociality relies heavily on the degree of relatedness[55]. Furthermore, as Boomsma (2009) pointed out, the empirical fact that obligate eusociality only ever evolved under conditions of strict lifetime monogamy serves as the ultimate phylogenetic vindication of inclusive fitness theory[12]. The controversy ultimately demonstrated that ecological pressures (group benefits) and kin selection (relatedness) are not competing hypotheses, but mathematically complementary requirements for the evolution of extreme altruism[4].

Implications for Living Together

Drawing sociological prescriptions for human beings from social insects is biologically fraught. Eusocial insects rely on haplodiploid genetics, female-only workforces, disposable males, and the complete suppression of individual reproduction in favour of a single ovary (the queen). The harmony of the hive is heavily reliant on a genetic identity (hyper-relatedness) that simply does not exist in human populations.

Human life-history evolution took a completely different path. As detailed by Kaplan, Hill, Lancaster, and Hurtado (2000, *Evolutionary Anthropology*), the human ecological niche is uniquely dependent on the extraction of high-quality, difficult-to-acquire resources (e.g., hunting, complex extractive foraging)[7]. This required an exceptionally extended juvenile period for brain development and skill acquisition[7]. To fund this prolonged, unproductive childhood, humans evolved a system of cooperative breeding characterised by long-term pair bonding and *complementary* male and female energetic investments, alongside intergenerational transfers from grandparents[7]. Unlike the expendable male drone, the human male is an essential provisioning and child-rearing partner whose caloric output peaks late in life[7].

Therefore, any attempt to model human gender roles, relationships, or family structures on the "hive" or the "queen" commits a glaring naturalistic fallacy. Natural does not mean good, and insect nature is fundamentally alien to human nature.

However, the organisational and computational mechanisms of social insects provide profound lessons for human groups, organisations, and societies:

1. **The Power of Decentralised Evaluation:** Like the bee swarm, human organisations make more accurate collective decisions when options are evaluated simultaneously and independently by multiple actors[47]. Relying on a single executive "scout" invites cascading errors; relying on a decentralised information market filters out individual noise.
2. **Constructive Cross-Inhibition:** Healthy debate requires mechanisms to actively suppress inferior ideas based on empirical verification (analogous to the stop signal)[47]. This prevents loud, early, but inaccurate voices from dominating the discourse and avoids decision deadlocks.
3. **Incentive Alignment and Enforced Altruism:** The tragedy of the commons is universally

destructive. In insects, it is solved by "enforced altruism" via worker policing[29]. In human societies, while we do not share the genetic relatedness that drives insect policing, cooperation must similarly be maintained by structuring environments that align individual incentives with collective goals, supported by social norms, transparency, and legal frameworks that actively punish defection and free-riding[61].

Summary of Robust Findings

1. Obligate eusociality in insects evolved exclusively in lineages possessing strict, lifetime monogamy, validating the necessity of high genetic relatedness (inclusive fitness) for the evolution of sterile castes.
2. Haplodiploidy results in a female-only workforce in Hymenoptera, relegating males solely to a brief reproductive role, whereas diplodiploid termites utilize both sexes.
3. Caste determination in honeybees is epigenetically controlled by nutrition; *Dnmt3* knock-downs (72% effect size) mimic the queen trajectory, proving the worker caste is an actively repressed state.
4. The "Royalactin" hypothesis for queen determination failed to replicate; instead, diet quantity (*ad libitum* feeding) and plant microRNA inhibitors are the primary physiological drivers.
5. Worker policing (the consumption of worker-laid eggs by nestmates) is a form of enforced altruism that resolves the tragedy of the commons in the hive, reducing worker-son survival to 0%.
6. Worker policing is most severe and effective in species where the queen mates multiply, as workers become more related to the queen's sons ($r = 0.25$) than to other workers' sons ($r = 0.125$).
7. Task allocation within the hive is driven by individual response thresholds to environmental stimuli, leading to age polyethism without central control, complemented by inactive "reserve" workers.
8. Honeybee swarms operate as a decentralised democracy, evaluating multiple nest sites and selecting the optimal one with ~80% accuracy based on strict volumetric and geographic criteria.
9. Swarms rely on a quorum threshold (~15 simultaneous bees at a site) rather than unanimous consensus to make final movement decisions, triggering a 200Hz piping signal for lift-off.
10. Cross-inhibition, via a 150ms vibratory "stop signal", is used to silence competing dancers, preventing decision deadlocks and filtering out individual sensory noise.

Contested or Open Questions

- **The Exact Nutritional Trigger for Queens:** If Royalactin is not the primary driver of caste determination, what is the precise molecular interplay between diet quantity (e.g., mTOR pathways) and dietary inhibitors (e.g., plant miRNAs in beebread) that triggers the epigenetic shift?
- **Redundancy in Chemical Signalling:** To what extent do cuticular hydrocarbons and

Dufour's gland secretions fully compensate for the absence of Queen Mandibular Pheromone (QMP) in regulating worker sterility across different environmental conditions?

- **The Maintenance of Inactive Workers:** Are "lazy" workers a genetically distinct sub-caste with permanently high response thresholds, or is their inactivity purely a stochastic function of spatial positioning and temporal demand within the nest?
- **Kin Selection vs. Multi-level Selection:** While the Nowak et al. (2010) paper was heavily rebutted, debates persist regarding the exact mathematical boundaries where inclusive fitness models fail and where trait-group selection models offer superior predictive power for the emergence of cooperation.

Most Important Sources to Read in Full

1. **Hamilton, W. D. (1964).** "The genetical evolution of social behaviour. I and II." *Journal of Theoretical Biology*.
2. **Hughes, W. O. H., Oldroyd, B. P., Beekman, M., & Ratnieks, F. L. W. (2008).** "Ancestral monogamy shows kin selection is key to the evolution of eusociality." *Science*.
3. **Boomsma, J. J. (2009).** "Lifetime monogamy and the evolution of eusociality." *Philosophical Transactions of the Royal Society B*.
4. **Wenseleers, T., & Ratnieks, F. L. W. (2006).** "Enforced altruism in insect societies." *Nature*.
5. **Seeley, T. D., Visscher, P. K., Schlegel, T., Hogan, P. M., Franks, N. R., & Marshall, J. A. R. (2012).** "Stop signals provide cross inhibition in collective decision-making by honeybee swarms." *Science*.
6. **Kucharski, R., Maleszka, J., Foret, S., & Maleszka, R. (2008).** "Nutritional control of reproductive status in honeybees via DNA methylation." *Science*.
7. **Buttstedt, A., Ihling, C. H., Pietzsch, M., & Moritz, R. F. A. (2016).** "Royalactin is not a royal making of a queen." *Nature*.
8. **Abbot, P., et al. (2011).** "Inclusive fitness theory and eusociality." *Nature*.
9. **Nowak, M. A., Tarnita, C. E., & Wilson, E. O. (2010).** "The evolution of eusociality." *Nature*.
10. **Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000).** "A theory of human life history evolution: Diet, intelligence, and longevity." *Evolutionary Anthropology*.

Works cited

1. The evolution of non-reproductive workers in insect colonies with, https://elifesciences.org/articles/08918
2. The Evolution of Social Evolution (Chapter 1) - Comparative Social, https://www.cambridge.org/core/books/comparative-social-evolution/evolution-of-social-evolution/65443293999C7C3CB06CC8A59EEE1C32
3. Evolution of eusociality - Wikipedia, https://en.wikipedia.org/wiki/Evolution_of_eusociality
4. Altruism, Spite, and Greenbeards, https://people.bu.edu/msoren/West.pdf
5. Breeding Biology of Reticulitermes aculabialis (Isoptera,

https://researcherslinks.com/current-issues/Breeding-Biology-Reticulitermes-acul abialis-Isoptera-Rhinotermitidae/20/1/5000/html
6. A theory of human life history evolution: Diet, intelligence, and, https://www.researchgate.net/publication/228558340_A_theory_of_human_life_history_evolution_Diet_intelligence_and_longevity
7. A Theory of Human Life History Evolution: Diet, Intelligence, and, https://www.unm.edu/~jlancas/KaplanHillLancasterHurtado_2000_LHEvolution.pdf
8. Lifetime monogamy and the evolution of eusociality - PMC - NIH, https://pmc.ncbi.nlm.nih.gov/articles/PMC2781870/
9. Inclusive fitness: 50 years on - Andy Gardner, https://gardner.wp.st-andrews.ac.uk/files/2015/05/GardnerWest_2014.pdf
10. Ancestral Monogamy Shows Kin Selection Is Key to the Evolution of, https://www.researchgate.net/publication/5338664_Ancestral_Monogamy_Shows_Kin_Selection_Is_Key_to_the_Evolution_of_Eusociality
11. Fig. 1. Phylogeny of genera of eusocial Hymenoptera (ants, bees, https://www.researchgate.net/figure/Phylogeny-of-genera-of-eusocial-Hymenoptera-ants-bees-and-wasps-for-which-female_fig2_5338664
12. Lifetime monogamy and the evolution of eusociality - ResearchGate, https://www.researchgate.net/publication/26871603_Lifetime_monogamy_and_the_evolution_of_eusociality
13. Nutritional Control of Reproductive Status in Honeybees via DNA, https://www.researchgate.net/publication/5512245_Nutritional_Control_of_Reproductive_Status_in_Honeybees_via_DNA_Methylation
14. Phenotypically distinct female castes in honey bees are defined by, https://genome.cshlp.org/content/28/10/1532
15. Epigenetics Mechanisms of Honeybees: Secrets of Royal Jelly - PMC, https://pmc.ncbi.nlm.nih.gov/articles/PMC10687967/
16. Life - Science News, https://www.sciencenews.org/article/life-10
17. Royalactin induces queen differentiation in honeybees, https://www.researchgate.net/publication/51073131_Royalactin_induces_queen_differentiation_in_honeybees_Biotechnology_Research_Center_Nature
18. Major royal jelly proteins of the honeybee Apis mellifera., https://www.mol-ecol.uni-halle.de/research/genomics/royal_jelly/
19. A sterility-associated long noncoding RNA involved in honey bee, https://www.pnas.org/doi/10.1073/pnas.2527882123
20. Diet quantity influences caste determination in honeybees (Apis, https://royalsocietypublishing.org/rspb/article/287/1927/20200614/85628/Diet-quantity-influences-caste-determination-in
21. Plant microRNAs in larval food regulate honeybee caste development, https://journals.plos.org/plosgenetics/article?id=10.1371/journal.pgen.1006946
22. Honeybees possess a structurally diverse and functionally, https://royalsocietypublishing.org/rspb/article/286/1905/20190517/85096/Honeybees-possess-a-structurally-diverse-and
23. New insights into honey bee (Apis mellifera) pheromone ... - PMC,

https://pmc.ncbi.nlm.nih.gov/articles/PMC2897789/
24. (PDF) Dufour's gland pheromone as a reliable fertility signal among, https://www.researchgate.net/publication/226707713_Dufour's_gland_pheromone_as_a_reliable_fertility_signal_among_honeybee_Apis_mellifera_workers
25. Worker policing - Wikipedia, https://en.wikipedia.org/wiki/Worker_policing
26. Worker Reproduction in Formica Ants | The American Naturalist, https://www.journals.uchicago.edu/doi/full/10.1086/518185
27. (PDF) Worker policing in the bee Apis florea - ResearchGate, https://www.researchgate.net/publication/225350416_Worker_policing_in_the_bee_Apis_florea
28. Worker policing in the German wasp Vespula germanica, https://academic.oup.com/beheco/article/19/2/272/212583
29. Comparative Analysis of Worker Reproduction and Policing in, https://www.journals.uchicago.edu/doi/full/10.1086/508619
30. Comparative Analysis of Worker Reproduction and Policing ... - Lirias, https://lirias.kuleuven.be/retrieve/84441086-7497-4f91-ad63-b46aba00028f
31. Worker reproduction and policing in insect societies: An ESS analysis, https://www.researchgate.net/publication/8399497_Worker_reproduction_and_policing_in_insect_societies_An_ESS_analysis
32. The evolution of extreme altruism and inequality in insect societies, https://royalsocietypublishing.org/rstb/article/364/1533/3169/21125/The-evolution-of-extreme-altruism-and-inequality
33. Anti-social punishment can prevent the co-evolution of ... - PMC, https://pmc.ncbi.nlm.nih.gov/articles/PMC3290516/
34. (PDF) Response threshold reinforcements and division of labour in, https://www.researchgate.net/publication/25453631_Response_threshold_reinforcements_and_division_of_labour_in_insect_societies
35. Response thresholds alone cannot explain empirical patterns ... - PMC, https://pmc.ncbi.nlm.nih.gov/articles/PMC8211278/
36. Fixed Response Thresholds and the Regulation of Division of Labor, https://www.researchgate.net/publication/23740482_Fixed_Response_Thresholds_and_the_Regulation_of_Division_of_Labor_in_Insect_Societies
37. Age polyethism can emerge from social learning: A game-theoretic, https://pmc.ncbi.nlm.nih.gov/articles/PMC12396761/
38. Response thresholds alone cannot explain empirical patterns of, https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.3001269
39. Individual experience influences reconstruction of division of labour, https://pmc.ncbi.nlm.nih.gov/articles/PMC9202139/
40. Who Are the “Lazy” Ants? The Function of Inactivity in Social Insects, https://www.researchgate.net/publication/323834448_Who_Are_the_Lazy_Ants_The_Function_of_Inactivity_in_Social_Insects_and_a_Possible_Role_of_Constraint_Inactive_Ants_Are_Corpulent_and_May_Be_Young_andor_Selfish
41. Who Are the “Lazy” Ants? The Function of Inactivity in Social Insects, https://academic.oup.com/icb/article/57/3/649/4036211
42. Behavioral and morphological traits influencing variation in task,

https://d-nb.info/1317483421/34
43. Honeybee Democracy 9781400835959 - DOKUMEN.PUB, https://dokumen.pub/honeybee-democracy-9781400835959.html
44. The Secret Life of Bees, https://research.annemariemaes.net/lib/exe/fetch.php?media=research:secret_life_of_bees.pdf
45. Setting up bait hives for beekeeping - Facebook, https://www.facebook.com/groups/wasatchbeekeepersassociation/posts/1334732783385782/
46. Nest-site selection in honey bees: How well do swarms implement, https://www.researchgate.net/publication/226809744_Nest-site_selection_in_honey_bees_How_well_do_swarms_implement_the_best-of-N_decision_rule
47. Honeybee Democracy (How 10,000 Bees Reach One Unanimous, https://apiaryproject.com/blog/honeybee-democracy-swarm-intelligence-decision-making
48. (PDF) Quorum sensing during nest-site selection by honeybee swarms, https://www.researchgate.net/publication/225491722_Quorum_sensing_during_nest-site_selection_by_honeybee_swarms
49. an experimental study of swarm guidance in the Western honey bee, https://journals.biologists.com/jeb/article/217/11/2020/12199/Moving-without-a-purpose-an-experimental-study-of
50. Scouting for bees - Ray Cannon's nature notes, https://rcannon992.com/2023/04/13/scouting-for-bees/
51. Stop Signals Provide Cross Inhibition in Collective Decision-Making, https://rangevoting.org/SeeleyVSHFMinhibit.pdf
52. Sensory coding of nest-site value in honeybee swarms, https://journals.biologists.com/jeb/article/211/23/3691/17956/Sensory-coding-of-nest-site-value-in-honeybee
53. The evolution of eusociality, http://courses.washington.edu/ccab/Nowak%20etal%20-%20evolution%20of%20eusociality%20-%20Nature%202010.pdf
54. The evolution of eusociality - PubMed - NIH, https://pubmed.ncbi.nlm.nih.gov/20740005/
55. New paper shows that Nowak et al. were wrong: kin selection, https://whyevolutionistrue.com/2015/03/27/new-paper-shows-that-nowak-et-al-were-wrong-kin-selection-remains-a-valuable-tool-in-evolutionary-biology/
56. Kin Selection and Its Critics | BioScience - Oxford Academic, https://academic.oup.com/bioscience/article/65/1/22/2754282
57. Eusociality: A Question of Mathematics or Bad Science?, https://www.bu.edu/writingprogram/journal/past-issues/issue-6/hammond/
58. THE THEORY OF INCLUSIVE FITNESS, https://openscholarship.wustl.edu/cgi/viewcontent.cgi?referer=&httpsredir=1&filename=0&article=1120&context=bio_facpubs&type=additional
59. THE EVOLUTION OF THE POST-REPRODUCTIVE LIFESPAN - UNM, http://www.unm.edu/~jwinking/PostRep2.pdf

60. The evolutionary and ecological roots of human social organization, https://royalsocietypublishing.org/rstb/article/364/1533/3289/21166/The-evolutionary-and-ecological-roots-of-human
61. The role of threats in animal cooperation - Royal Society Publishing, https://royalsocietypublishing.org/rspb/article/278/1703/170/73428/The-role-of-threats-in-animal-cooperationReview