

The Nutritional Gap: Why Mono-Origin Pollen Is Insufficient for Commercial Honey Bee Colonies

...and how full-spectrum supplemental nutrition bridges the gap

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EXECUTIVE SUMMARY

Commercial honey bee colonies increasingly operate in nutritional environments for which evolution did not prepare them. Migratory pollination routes — from California almonds to Pacific Northwest blueberries to Florida and Southeastern crops — place tens of thousands of colonies inside single-crop monocultures for weeks at a time. Sideline operations face a parallel challenge: intensified agricultural landscapes and seasonal forage gaps that eliminate the floristic diversity on which healthy bee nutrition depends.

The result in both cases is the same: colonies subsisting on mono-origin or severely restricted pollen sources cannot achieve the full-spectrum macronutrient, essential amino acid, lipid, sterol, and micronutrient balance that peer-reviewed research has established as necessary for brood development, fat-body reserves, immune function, and detoxification capacity.

This white paper reviews the scientific evidence for the nutritional inadequacy of mono-origin pollen, explains the specific biological mechanisms through which nutritional deficiencies compromise colony performance, and describes how VitalBee™ — a full-spectrum supplemental bee feed developed by Natural Bee Care, LLC — is formulated to address each documented gap.

KEY FINDING

Landscape change and the disappearing forage base — the simplification of agricultural landscapes from diverse polycultures into mono-crop production, the loss of uncultivated forage margins, and the compression of seasonal bloom windows — is the structural driver behind the nutritional, immune, and pollination-performance challenges facing both commercial operators and sideliners. Supplemental nutrition is not a compensation for poor bee-keeping practice; it is the recognition that the landscape no longer provides what bee colonies require.

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1. The agricultural context: when monoculture becomes a nutritional trap

Honey bees evolved as generalist foragers across diverse floral landscapes. A colony in a temperate mixed environment typically visits dozens of plant species across a foraging season, assembling a diet that is nutritionally complementary across sources — high-protein pollens balanced against lipid-rich ones, sterols from one species supplementing those lacking in another.

Modern commercial beekeeping has fundamentally altered this dynamic. The United States almond industry alone requires approximately 2.6 to 2.8 million managed colonies each February — the majority of all commercially managed US colonies — placed inside vast monocultures of a single crop. Subsequent routing through blueberry, avocado, cranberry, and clover pollination contracts continues the pattern of prolonged single-crop exposure. The problem is not merely one of pollen scarcity; it is a problem of nutritional monoculture.

Bryś and Strachecka (2024) summarize the structural problem directly: vast agricultural acreages dominated by mono-crop plants force bees into “*a mono diet — which results in their malnutrition.*” Their systematic review in *Molecules* documents that even high-protein crops such as rapeseed (27% crude protein) fail to deliver complete essential amino acid balance, while low-protein crops such as buckwheat (11%) present colony-threatening nutritional short-

falls. The pollen protein content of a crop tells only part of the story; amino acid profile, lipid composition, and sterol content determine whether that protein can actually be utilized.

Sideline and hobbyist operations face a related but distinct version of the problem. Landscape intensification — the conversion of hedgerows, meadows, and mixed-use agricultural margins to continuous monoculture — progressively narrows the forage diversity available even to stationary apiaries. Seasonal dearth periods, which now extend longer and arrive earlier in many regions due to climate-driven shifts in bloom phenology, create windows of nutritional crisis that a single forage crop cannot bridge.

The consequence in both commercial and sideline contexts is a colony in chronic or periodic nutritional deficit — capable of survival, but not capable of the metabolic performance that peak pollination, peak brood production, and peak disease resistance require.

2. Essential amino acid deficiency: the primary bottleneck

2.1 The de Groot framework and its commercial relevance

The foundational scientific framework for honey bee amino acid requirements was established by de Groot (1953), whose work in *Physiologia Comparata et Oecologia* identified all ten essential amino acids required by *Apis mellifera* and their proportional requirements for optimal colony function. For seventy years, this research has guided the interpretation of pollen quality and the formulation of supplemental feeds.

Randy Oliver and co-investigators at USDA-ARS extended de Groot's framework into the commercial field context (Ricigliano, Williams & Oliver, 2022). Their study, conducted across a northern California commercial beekeeping operation from August through February, found that diet macronutrient content alone was not correlated with colony size or health biomarkers. What did matter was the pattern of essential amino acid deficiencies relative to leucine — the most abundant EAA in bee protein requirements. The sum of those deficiencies showed significant correlation with February colony strength — the metric that determines commercial almond pollination readiness.

This finding has practical implications that the industry has been slow to absorb. A feed with adequate crude protein but imbalanced EAA ratios will not achieve the colony performance that a well-balanced, lower crude-protein feed will. Isoleucine and methionine are the most commonly limiting amino acids in commercial plant-protein substitutes — meaning that however much protein a colony consumes, brood development and fat-body recovery are constrained at those two bottlenecks.

2.2 The consequences of EAA imbalance: from individual bee to colony

The downstream consequences of essential amino acid deficiency cascade across every level of colony organization. At the individual level, Brys and Strachecka (2024) document that unavailability of even a single essential amino acid can be a limiting factor for individual bee development. Metabolites formed through protein digestion are central to energy production; when the amino acid chain is incomplete, that metabolic pathway is throttled.

At the colony level, the effects are measurable in the key physiological markers used to assess colony health. Vitellogenin — the glycolipoprotein produced in the fat body that serves as nurse bee storage protein, immune modulator, and longevity regulator — is “highly expressed in nurses as compared to foragers” and its synthesis depends directly on the availability and quality of dietary protein (Alaux et al., 2010; Barraud et al., 2023). Colonies on nutritionally deficient diets show reduced vitellogenin expression, smaller hypopharyngeal glands, impaired immune function, and shorter individual lifespans. Each of these deficits compounds across the colony’s population and across the pollination season.

The research of Vaudo et al. (2020) on EAA compensatory foraging adds a further dimension: colonies lacking complete EAA supply increase foraging effort in an attempt to close the nutritional gap. This behavioral response — bees working harder to find what the environment cannot provide — represents a metabolic cost paid at the expense of other colony functions, and fails entirely when the monoculture environment has no complementary forage to offer.

| Essential amino acid | Primary biological role in honey bees |
|----------------------|---|
| Leucine | Reference EAA for proportional balance; central to protein synthesis signaling. |
| Arginine | Immune signaling, wound healing, brood development. |
| Isoleucine | Energy metabolism; most commonly deficient AA in commercial substitutes. |
| Methionine | Sulfur-containing; detoxification pathways; most common limiting AA in bee diets. |
| Lysine | Growth and structural proteins; absorption rate-limiting in some formulations. |
| Valine | Cellular metabolism; commonly deficient in plant-protein feeds. |
| Threonine | Often inadequate in plant-protein formulations. |
| Histidine | Enzyme function, hemolymph buffering. |
| Phenylalanine | Cuticle hardening; tyrosine precursor. |
| Tryptophan | Serotonin / melatonin pathways; difficult to measure due to acid-hydrolysis loss. |

Table 1. All ten essential amino acids and their primary biological roles in *Apis mellifera*. Sources: de Groot (1953); Oliver (2014–2023); Ricigliano, Williams & Oliver (2022).

3. The lipid and sterol deficit: what protein alone cannot provide

3.1 Omega fatty acids and fat body function

Protein receives the majority of attention in bee nutrition research, but lipids — particularly fatty acid composition and balance — are equally determinative of colony health outcomes under commercial stress conditions. Pollen lipids serve as the primary substrate for nurse-bee fat-body development, brood provisioning, and the regulation of immune response pathways.

Research published in the *Journal of Experimental Biology* (Grozinger et al., 2021) established a direct link between pollen lipid composition and insecticide resilience. Diets with lower pollen protein-to-lipid ratios mitigated the effects of organophosphate pesticides on honey bee survival and physiology. For colonies operating in commercial pollination environments — where pesticide exposure is an operational baseline rather than an exceptional event — this relationship between dietary lipid adequacy and pesticide tolerance is not academic.

Subsequent work on fat-body lipogenic capacity in honey bee workers (Groh et al., 2024, *Journal of Experimental Biology*) extended this understanding: the capacity of nurse bees to synthesize and store lipids in the fat body is a central determinant of their ability to provision larvae, sustain royal jelly production, and survive the metabolic demands of overwintering and migratory stress. Pollen diversity — or its functional equivalent in a supplemental feed — is required to support the full range of fatty acid substrates that fat-body lipogenesis requires.

3.2 Phytosterols: the nutritional element that sugar and crude protein cannot substitute

Perhaps the most underappreciated dimension of honey bee nutritional requirements is the sterol deficit inherent in mono-origin and pollen-poor diets. Honey bees, in common with all insects, are sterol auxotrophs — they are biologically incapable of synthesizing sterols de novo from carbohydrate or protein precursors. Every sterol molecule used in larval cuticle formation, molting hormone production, and cellular membrane maintenance must come from dietary sources. In practice, that means pollen.

Cardoza et al. (2020), in research published in *Molecules* (MDPI), identified 24-methylenecholesterol as the key phytosterol required by honey bees. Nurse bees assimilate this sterol from dietary sources and store it in their tissues as endogenous sterol, which is then selectively transferred to developing larvae through brood food secreted from the hypopharyngeal and mandibular glands. The study demonstrated significantly higher survival, diet consumption, head protein content, and abdominal lipid content in sterol-supplemented bees compared to controls.

Svoboda et al. (1982) had earlier established a complementary finding: honey bees are among the very few phytophagous insects incapable of converting C-24 alkyl phytosterols to cholesterol. The primary tissue sterol of honey bee brood is always 24-methylenecholesterol, regardless of what other sterols are available in the diet. This metabolic constraint means that a mono-origin pollen source — even one with adequate crude protein — may fail to deliver adequate 24-methylenecholesterol if that species does not produce it at functional levels. Multiple pollen sources, or a supplemental feed with functional sterol inclusion, is not a preference; it is a *metabolic necessity*.

Why sugar and soy protein cannot fill the sterol gap. Commercial “sugar and protein” feeds — the industry baseline — contain no phytosterols. Bees cannot synthesize sterols from sugar or crude protein. A colony fed only sugar syrup and soy-based protein supplement during a pollen dearth will produce brood with sterol-deficient cuticle and impaired molting capacity. This deficit is invisible in short-term colony counts but manifests in reduced brood survival and compromised adult bee quality.

4. Detoxification capacity: nutrition as pesticide defense

The intersection of pesticide exposure and nutritional status is one of the most consequential and least-discussed dimensions of commercial bee health management. Migratory pollination places colonies in environments where pesticide residues are not incidental but structural — residues from prior crop applications persist in wax and pollen stores, and new applications occur during and after bloom windows.

The detoxification mechanism in honey bees operates through Phase I cytochrome P450 enzymes and Phase II conjugation pathways, with activity levels that are directly responsive to nutritional inputs. Du Rand et al. (2015) demonstrated in *Scientific Reports* that honey bee tolerance of toxic compounds — using dietary nicotine as an experimental model — is mechanistically dependent on detoxification enzyme activity, and that nutritional status directly modulates this capacity. This research established the biochemical pathway through which nutritional adequacy becomes pesticide resilience.

The Grozinger et al. (2021) findings at Penn State reinforce this connection at the dietary level: the protein-to-lipid ratio of pollen — not just crude protein quantity — shapes how effectively bee detoxification pathways respond to organophosphate exposure. Bees on nutritionally balanced diets with optimized lipid profiles showed measurably better survival under insecticide challenge than bees on protein-dominant, lipid-deficient diets.

For the commercial beekeeper moving colonies through almond, blueberry, and avocado pollination cycles, this relationship has direct operational implications: the nutritional status of colonies entering each pollination window determines not just their foraging output but their capacity to survive and recover from the pesticide exposures that are part of every commercial contract environment.

Phytochemicals — present in diverse pollen sources and replicable in formulated supplemental feeds — play a supporting role in both Phase I and Phase II detoxification. Quercetin, kaempferol, and related flavonoids present in pollen from diverse plant sources have been documented to upregulate P450 activity in honey bee tissues. A mono-origin pollen source eliminates this phytochemical diversity, with consequences for detoxification capacity that compound across a multi-contract season.

5. Pollen diversity and the immune-nutritional interface

The relationship between pollen diversity and colony immune competence has emerged as a

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robust finding in the apicultural research literature of the past decade. Alaux et al. (2010), in a landmark study published in *Functional Ecology*, established that the diversity of pollen diets directly influenced the activity of glucose oxidase — an enzyme critical to honey bee immune response — and that colonies on diverse pollen diets showed enhanced resistance to *Nosema ceranae* infection.

This work was extended by Barraud et al. (2023), whose research on pollen nutrition and honey bee health — including the metabolomic profiling study published in *Metabolomics* — documented that pollen diet composition shapes the bee metabolome in ways that extend well beyond simple macronutrient accounting. The identity and balance of pollen sources, not just their protein quantity, determines the array of bioactive compounds available for immune function, oxidative stress management, and gut microbiome support.

The study by Barraud and colleagues examining pollen diet and microbiome interactions (*Scientific Reports*, 2025) adds a further dimension: pollen nutrition influences the composition of the honey bee gut microbiota, with downstream effects on nutrient absorption efficiency, immune signaling, and pathogen resistance. A nutritionally impoverished mono-origin pollen environment thus compromises colony health through multiple simultaneous pathways.

For operations managing colonies through the stress profile of migratory pollination — transport stress, new environments, pesticide loads, and temperature extremes — this immune-nutritional interface is not a background variable. It is the mechanism through which nutritional investment translates, or fails to translate, into commercial performance.

6. The sideline beekeeper: landscape change and the disappearing forage base

The nutritional challenges facing sideline and hobbyist beekeepers are structurally different from those of migratory commercial operations but converge on the same metabolic deficits. Rather than mono-crop immersion, sideline beekeepers face the progressive impoverishment of the agricultural landscape — the replacement of diverse forage with managed monocultures,

What's actually in a commercial pollen patty?

The “real pollen” fraction in most commercial bee feeds — typically 10–15% by label — is overwhelmingly *Brassica napus* (rapeseed) imported from China, a byproduct of oil-crop production. Pure rapeseed pollen produces the poorest colony development of any single-source pollen tested in trial conditions (Bryś & Strachecka, 2024) — the same mono-floral problem this paper documents, transferred into the supplement itself.

Two pathways compound the issue. Methionine — the first limiting amino acid in bee diets — drops to undetectable levels after 15 months in dried pollen (Bryś et al., 2025); the China-to-US patty supply chain routinely exceeds that window. And a 2018 survey of Chinese pollen samples detected persistent contamination with neonicotinoid insecticides, in-hive acaricides, and broad-spectrum fungicides at hazard-quotient levels >50 (Tong et al., 2018) — the same load Section 4 argues colonies must detoxify, not consume.

Sources: Bryś & Strachecka, *Molecules* 2024; Bryś et al., *Foods* 2025; Tong et al., *STOTEN* 2018.

the loss of uncultivated margins and hedgerows, and the compression of bloom windows due to synchronized crop management.

Barraud et al. (2023) document that bees in nutritionally restricted environments — including those created by landscape simplification rather than deliberate management — show measurable metabolomic signatures of stress: altered fatty acid profiles, reduced vitellogenin levels, and downregulated detoxification capacity. These signatures appear before colony-level health metrics deteriorate visibly, meaning that by the time a sideline beekeeper observes reduced colony performance, the nutritional deficit has been accumulating for weeks or months.

The seasonal dimension is equally important for sideline operations. Mid-summer and early fall dearth periods — when most agricultural crops are past peak bloom and natural forage is diminished — represent windows of nutritional vulnerability that can determine whether colonies build adequate winter reserves. A colony entering fall with depleted fat bodies and insufficient protein reserves will not survive winter at the rates a well-nourished colony will, regardless of Varroa treatment status or disease load.

The research of Strachecka and colleagues documents a direct relationship between amino acid composition in the hemolymph, colony strength, honey yield, and successful overwintering. For the sideline beekeeper, supplemental nutrition during forage gaps is not a compensation for poor management — it is the recognition that the landscape no longer provides what bees require.

7. The VitalBee™ response: full-spectrum formulation principles

VitalBee™ is formulated against the nutritional science reviewed in the preceding sections — not against the lowest-cost path to colony survival, but against the metabolic performance requirements that the peer-reviewed literature has established as necessary for commercial and sideline beekeeper success.

Three deliberate formulation choices distinguish VitalBee™ from standard sugar-and-protein feeds:

7.1 Complete essential amino acid balance

All ten essential amino acids are present at levels calibrated to the de Groot / Randy Oliver framework, with particular attention to the historically deficient amino acids isoleucine and methionine that constrain brood development and fat-body recovery in plant-protein substitutes. Total EAAs represent 32.8% of crude protein — within Oliver's established 30–50% optimal range. The sum of EAA deficiencies relative to leucine, the metric found by Ricigliano et al. (2022) to be the strongest predictor of February colony strength, has been minimized across the formulation.

7.2 Optimized lipid profile with functional sterol inclusion

A 4:1 omega-3 to omega-6 fatty acid ratio, ALA-rich at 21,393 mg per patty, supports nurse-bee fat-body reserves and brood development while aligning with the lipid-to-protein ratios associated with improved pesticide resilience in the Grozinger et al. (2021) research. Phytosterols are

included at functional levels — addressing the sterol auxotrophy that makes diversified pollen or deliberate sterol supplementation a metabolic necessity rather than a formulation preference.

7.3 Functional micronutrient and phytochemical complex

Beyond the macronutrient profile: phytochemicals supporting Phase I and Phase II detoxification pathways for clearance of pesticide residues common in commercial pollination environments; an antioxidant complex for oxidative- and heat-stress resilience; and a complete trace-mineral profile calibrated for the metabolic demands of migratory pollination. Phosphorus (921 mg per patty), magnesium, zinc, and a full B-vitamin panel support the enzymatic activity that immune function and detoxification require.

| Nutritional component | Amount per 454 g patty |
|--------------------------------------|----------------------------|
| Calories | 1,507 kcal |
| Crude protein | 65.8 g (17.4% DM) |
| Total lipid (fat) | 51.0 g (13.5% DM) |
| Omega-3 fatty acids (ALA) | 21,393 mg |
| Omega-3 : omega-6 ratio | 4:1 |
| Carbohydrate (incl. added sugar) | 225.7 g (59.7% DM) |
| Dietary fiber (from plant protein) | 42.9 g |
| Total essential amino acids (all 10) | 21.58 g (32.8% of protein) |
| Phosphorus | 921 mg |
| Zinc | 6.32 mg |

Table 2. VitalBee™ macronutrient and micronutrient profile per finished 1 lb (454 g) patty. Values are typical for finished product; minor batch variation is normal. Source: Natural Bee Care, LLC, Technical & Commercial Product Brief (2026).

8. Field evidence and emerging trial data

Controlled trials with published statistical significance are in progress through the 2026–2027 season. The field observations reported here represent structured reports from named commercial operators with documented colony counts, on file with Natural Bee Care, LLC. They are presented as indicative observations, not controlled study results.

Russell Heitkam (4,000 colonies, Northern California): Full 1 lb patties consumed within ten days with no waste, consistent across placement sites.

Justin Brown (25+ year commercial beekeeper): Struggling colonies consuming approximately 2 lb over 2.5 weeks, followed by visible colony expansion and population recovery.

Donna Shea (Honey Bee Initiative, George Mason University): Strong brood patterns and measurable colony growth through significant weather variability; colonies reached split-ready strength within weeks of feeding.

North Carolina structured comparison, Spring 2026: Across 300 nucleus colonies compared against a leading commercial patty competitor and a probiotic treatment, VitalBee-fed nucs showed strong consumption and brood development outcomes. One incidental observation — absence of hive beetle colonization in VitalBee-fed nucs at assessment, while presence was observed in comparison groups — is noted as a hypothesis-generating observation warranting formal investigation, not a product claim.

The 2026–2027 formal trial program includes 24-hour, 7-day, and 14-day controlled consumption-rate studies under varying ambient temperatures; brood development and colony-strength comparisons against named commercial competitors; and follow-up investigation of the hive-beetle observation. Results will be made available to commercial cooperators and prospective buyers as completed.

9. Implications for commercial and sideline practice

The nutritional research reviewed here converges on a practical conclusion: supplemental nutrition for honey bee colonies is most effective when it is full-spectrum — addressing amino acid balance, lipid profile, sterol provision, and micronutrient completeness simultaneously — and least effective when it addresses only the single-variable benchmarks (crude protein, crude calories) that commercial feed products have historically optimized.

For migratory commercial operators, the pre-bloom build phase is the highest-leverage intervention point. The Ricigliano et al. (2022) data showing that EAA balance in fall and early winter feeding directly predicts February almond pollination strength establishes the causal chain: nutritional investment made weeks before colonies are deployed determines whether those colonies arrive at contract strength or spend the bloom window still building population. VitalBee™ is designed for use across the full seasonal program — pre-bloom build, in-bloom maintenance, and post-bloom recovery — because the research literature supports continuous nutrition management rather than episodic supplementation.

For sideline beekeepers, the practical application is nutritional bridging during forage gaps. Supplemental nutrition during summer dearth and fall pollen scarcity is not a substitute for good landscape stewardship — but it is the most direct available response to landscapes that no longer provide the forage diversity that colony health requires. The fat-body reserves that bees build in late summer and early fall are the reserves that determine winter survival rates; building those reserves requires complete nutrition, not just calories.

10. Conclusions

The scientific literature is clear: mono-origin pollen is nutritionally inadequate for honey bee colonies operating under commercial pollination or landscape-impooverished sideline conditions. The inadequacy is not simply a matter of protein quantity — it is a multi-dimensional deficit

spanning essential amino acid balance, lipid and sterol provision, phytochemical diversity, and micronutrient completeness.

Each dimension of this deficit has documented consequences for brood development, fat-body reserves, detoxification capacity, immune function, and colony resilience under the stressors — pesticide exposure, transport stress, pathogen pressure, thermal extremes — that define modern managed bee operations.

Full-spectrum supplemental nutrition, formulated against the specific nutritional requirements that the peer-reviewed research literature has established, is the most direct and evidence-supported response available to beekeepers. VitalBee™ represents an application of that research to commercial practice: a feed engineered not for minimum viable colony survival, but for the metabolic performance that commercial pollination, productive sidelining, and long-term colony health require.

About Natural Bee Care, LLC

Natural Bee Care, LLC is the manufacturer of VitalBee™, a full-spectrum honey bee supplemental feed formulated to meet the macronutrient, essential amino acid, lipid, sterol, and trace-mineral requirements of commercial pollinators under real-world stress. VitalBee™ is produced in Butte, MT and is available in 1 lb patties, by the case (40 lb), pallet, and full truckload for domestic and export markets. For product, trial, and purchasing information: vitalbeefeed.com

References

- Alaux, C., Ducloz, F., Crauser, D. & Le Conte, Y. (2010). Diet effects on forager bee health. *Functional Ecology*, 24(4), 791–800. <https://doi.org/10.1111/j.1365-2435.2010.01768.x>
- Barraud, A., Barascou, L., Lefebvre, V. et al. (2023). A metabolomics approach to the study of honey bee nutritional status and its link to gut microbiota. *Metabolomics*, 19, 61. <https://doi.org/10.1007/s11306-023-02039-1>
- Barraud, A. et al. (2025). Unravelling pollen diet and microbiome influence on honey bee health. *Scientific Reports*, 15, 13547. <https://doi.org/10.1038/s41598-025-96649-5>
- Bryś, M.S. & Strachecka, A. (2024). The key role of amino acids in pollen quality and honey bee physiology — a review. *Molecules*, 29(11), 2605. <https://doi.org/10.3390/molecules29112605>
- Bryś, M.S. et al. (2025). Changes in the amino acid composition of bee-collected pollen during 15 months of storage in fresh-frozen and dried forms. *Foods*, 15(2), 207.
- Cardoza, Y.J., Sheng, Z. & Bhatt, S. (2020). Novel insights into dietary phytosterol utilization and its fate in honey bees (*Apis mellifera* L.). *Molecules*, 25(3), 571. <https://doi.org/10.3390/molecules25030571>
- de Groot, A.P. (1953). Protein and amino acid requirements of the honeybee. *Physiologia Comparata et Oecologia*, 3(2–3), 197–285.
- du Rand, E.E., Smit, S., Beukes, M., Apostolides, Z., Pirk, C.W.W. & Nicolson, S.W. (2015). Detoxification mechanisms of honey bees (*Apis mellifera*) resulting in tolerance of dietary nicotine. *Scientific Reports*, 5, 11779. <https://doi.org/10.1038/srep11779>
- Groh, C.A., Aumer, D., Grozinger, C.M. et al. (2024). Fat body lipogenic capacity in honey bee workers. *Journal of Experimental Biology*, 227(18), jeb247777. <https://doi.org/10.1242/jeb.247777>
- Grozinger, C.M. et al. (2021). Pollen protein and lipid content influence resilience to insecticides in honey bees (*Apis mellifera*). *Journal of Experimental Biology*, 224(9), jeb242040. <https://doi.org/10.1242/jeb.242040>

- Hesketh-Best, P.J. et al. (2025). Pollen diet and sterol provisioning differentially affected larval development in a generalist solitary bee. *bioRxiv*. <https://doi.org/10.1101/2025.04.21.649687>
- Oliver, R. (2014–2023). Protein nutrition of honey bees [series]. ScientificBeekeeping.com.
- Ricigliano, V.A., Williams, S.T. & Oliver, R. (2022). Effects of different artificial diets on commercial honey bee colony performance, health biomarkers, and gut microbiota. *BMC Veterinary Research*, 18, 34. <https://doi.org/10.1186/s12917-022-03151-5>
- Sułkowska, et al. (2024). Gamma irradiation and ozone application as preservation methods for longer-term storage of bee pollen. *Foods*.
- Svoboda, J.A., Thompson, M.J., Herbert, E.W. & Shimanuki, H. (1982). Selective sterol transfer in the honey bee: Its significance and relationship to other Hymenoptera. *Lipids*, 17(5), 400–405.
- Tong, J. et al. (2018). A survey of multiple pesticide residues in pollen and beebread collected in China. *Science of the Total Environment*.
- Vaudo, A.D. et al. (2020). Pollen protein:lipid macronutrient ratios may guide broad patterns of bee species floral preferences. *Insects*, 11, 132. <https://doi.org/10.3390/insects11020132>
- Wright, G.A., Nicolson, S.W. & Shafir, S. (2018). Nutritional physiology and ecology of honey bees. *Annual Review of Entomology*, 63, 327–344. <https://doi.org/10.1146/annurev-ento-020117-043423>