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Influence of Colony State, Genetic Background, and Larval Origin on Queen Cell Acceptance and Royal Jelly Yield in *Apis mellifera*

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Abstract: Commercial queen rearing and royal jelly production represent economically significant sectors of modern apiculture, yet the interactive effects of colony state, genetic lineage, and larval provenance on these processes remain incompletely characterized. This study evaluated the individual and synergistic influences of colony state (queenless vs. queenright), subspecies hybrid (Italian ***A. m. ligustica*** vs. **Carniolan *A. m. carnica***), and grafted larval origin on queen cell acceptance rates and royal jelly production efficiency. Young worker larvae (<24 h post-eclosion) from both genetic backgrounds were grafted into artificial queen cups and introduced into standardized cell-builder colonies during peak nectar flow. Results demonstrated that colony state exerted the most significant influence on acceptance rates, with queenless colonies achieved 61.8% acceptance rate compared to 58.5% in queenright colonies ($P<0.05$). Italian hybrid colonies exhibited superior acceptance rates (64.0%) compared to that of Carniolan hybrids (56.3%, $P<0.05$), while larval origin showed no significant effect on initial acceptance ($P>0.05$), suggesting minimal genetic discrimination by nurse bees during early queen cell provisioning. Royal jelly yield per accepted cell was significantly higher in queenless colonies (150.1 mg) versus queenright colonies (143.7 mg, $P<0.05$), whereas neither colony hybrid nor larval origin significantly affected royal jelly production ($P>0.05$). These findings indicate that colony state and genetic background of nurse bee populations are primary determinants of queen rearing efficiency and royal jelly productivity, whereas larval genetic provenance plays a negligible role. The results have practical implications for optimizing commercial queen production and royal jelly harvesting protocols.

Keywords: *Apis mellifera*, queen rearing, royal jelly production, grafting technique, subspecies hybrid, colony state, emergency response.

1. Introduction

Honey bee (***Apis mellifera***) provides indispensable pollination services for global agriculture while generating economically valuable hive products, including honey, pollen, propolis, beeswax, venom, and royal jelly (**Klein *et al*., 2007**). Among these products, royal jelly-a proteinaceous secretion of hypopharyngeal and mandibular glands in nurse bees-commands premium market value due to its nutritional composition and pharmacological properties (**Ramadan and Al-Ghamdi, 2012**). Concurrently, commercial queen production represents a specialized apicultural practice essential for maintaining genetic improvement programs and supporting the beekeeping industry. Both queen rearing and royal jelly production mimic the colony's natural emergency response mechanism, wherein workers are stimulated to construct queen cells and provision larvae with royal jelly following queen loss (**Laidlaw and Page, 1997**). However, the efficiency of this controlled artificial system depends on multiple interacting factors including colony genetic composition, strength of the colony, nutritional status, and-most importantly-the presence or absence of a viable queen (**Winston, 1987**). The colony's genetic background, determined by subspecies or hybrid lineage, profoundly influences behavioral and physiological characteristics including brood-rearing patterns, foraging activity, and reproductive tendencies (**Ruttner, 1988**). Colony queen state (presence or absence of a laying queen) represents another pivotal factor modulating worker behavior **(Büchler *et al*., 2013)**. Queenless colonies initiate an emergency response characterized by accelerated queen cell construction, enhanced provisioning of royal jelly and also increased acceptance rates of grafted cups (**Free, 1987; Pettis *et al*., 1998**). Conversely, queenright colonies maintain reproductive suppression through queen-produced pheromones, particularly queen mandibular pheromone (QMP), which inhibits queen cell initiation and modulates worker ovarian development (**Pankiw *et al*., 1998 and Hoover *et al*., 2003**). Despite widespread commercial adoption of both queenless and queenright systems, comparative assessments of their relative efficacy remain limited. Among ***A. mellifera*** subspecies, Italian bees (***A. m. ligustica***) and Carniolan bees (***A. m. carnica***) dominate commercial beekeeping operations globally. Italian bees are characterized by prolific brood production, large colony populations, and sustained foraging activity under abundant nectar conditions (**Guzmán-Novoa *et al*., 2010**), whereas Carniolan bees exhibit rapid spring buildup, reduced swarming propensity (relative to other subspecies), and exceptional gentleness (**Rinderer, 1986**). These inherent behavioral and physiological differences may be translated into differential efficiency in queen rearing and royal jelly production systems. The possible interaction between the grafted larvae's (larval origin) and nurse bees' (colony hybrid) genetic origins is a factor that has received less attention. Despite the fact that honey bees have kin recognition systems, it is unknown if nurse bees prefer or treat their own larvae differently. According to the theory of kin recognition in social insects, workers may raise related larvae more frequently than unrelated ones (**Page and Erickson, 1986**). This begs the question of whether nursing bees from an Italian-hybrid colony, for instance, would accept and supply larvae of Carniolan ancestry as readily as they would their own family in the context of queen raising. Subtle biases may affect acceptance rates and the quality of queens produced, even though the superorganism model suggests that colony demands frequently take precedence over individual kin preferences (**Tarpy *et al*., 2004**).

This study aimed to quantify the individual and interactive effects of colony state (queenless vs. queenright), colony genetic background (Italian vs. Carniolan hybrid), and larval origin (Italian vs. Carniolan) on: (1) acceptance rates of grafted queen cells, and (2) royal jelly production per accepted cell. We hypothesized that: (1) queenless colonies would exhibit higher acceptance rates and royal jelly yields due to enhanced emergency response; (2) genetic background would influence both metrics through subspecies-specific behavioral traits; and (3) nurse bees would demonstrate kin-biased acceptance or provisioning favoring conspecific larvae.

2. Materials and Methods

2.1. Study Location and Timing

The experiment was conducted at the Apicultural Research Department, Sakha Agricultural Research Station, Kafr El-Sheikh Governorate, Egypt during the 2024 active season. All procedures were

performed during the primary nectar flow period (March-May) to ensure optimal forage availability and colony physiological condition.

2.2. Experimental Design

A full factorial design with three factors was implemented:

- **Factor 1 (Colony State):** Queenless vs. Queenright
- **Factor 2 (Colony Hybrid):** Italian (***A. m. ligustica***) vs. Carniolan (***A. m. carnica***)
- **Factor 3 (Larval Origin):** Italian vs. Carniolan

2.3. Colony Preparation and Standardization

Twelve honey bee colonies of comparable strength were selected and standardized 30 days prior to experimental manipulation. Each colony was equalized to contain: (i) eight frames of all-stages brood (eggs, larvae, and sealed brood); (ii) two frames of food reserves (adequate honey and pollen stores); and (iii) adequate adult bee coverage. All colonies were housed in standard 10-frame Langstroth hives with identical management protocols. Queens in all colonies were naturally-mated, age-matched (1-year-old), and actively laying at experimental initiation.

Queenless Treatment: Colony queens were removed 24 hours prior to grafted larvae introduction and any naturally-initiated emergency queen cells were destroyed.

Queenright Treatment: Queens were confined to the lower brood chamber using a vertical queen excluder and the grafted larvae were placed in the upper, queen free champers.

2.4. Larval Source and Grafting Procedure

Two breeder colonies (one Italian hybrid, one Carniolan hybrid) of confirmed genetic background and superior productivity were selected as larval sources. Newly deposited eggs in these colonies were marked and monitored until larval eclosion (72 hours). First-instar larvae (12-24 hours post-eclosion) were grafted using a grafting needle into plastic queen cups (Jenter™ system) mounted on wooden cell bars (30 cups per bar).

Grafting Protocol:

1. Cell bars with empty queen cups were introduced to recipient colonies 2 hours pre-grafting to allow surface conditioning and acceptance.
2. In queenless colonies, cell bars were positioned centrally between two frames of emerging brood in the brood chamber
3. In queenright colonies, cell bars were placed between brood frames in the upper (queen-excluded) chamber

2.5. Response Variables and Data Collection

2.5.1. Queen Cell Acceptance Rate

Twenty-four hours post-grafting, cell bars were carefully removed for inspection. A cell was scored as "accepted" if: (i) the grafted larva remained present, (ii) visible royal jelly accumulated at the cell base, and (iii) cell wax walls showed evidence of worker attention (elongation or polishing). Acceptance rate was calculated as:

$$\textbf{Acceptance Rate (\%)} = \textbf{(Number of Accepted Cells / Total Grafted Cells)} \times \textbf{100}$$

2.5.2. Royal Jelly Production

Seventy-two hours post-grafting (optimal timing for maximal royal jelly accumulation; **Haddad *et al.*, 2007**), accepted queen cells were harvested. Larvae were gently removed using a curved needle, and

royal jelly was individually extracted from each cell using a sterile wooden spatula. Samples were immediately transferred to pre-weighed microcentrifuge tubes and weighed on an analytical balance (±0.001 g precision, Sartorius BP211D). Royal jelly yield was calculated as:

Royal Jelly Yield (mg/cell) = Total Royal Jelly Mass (mg) / Number of Accepted Cells

The grafting cycle was repeated at 72-hour intervals throughout the experimental period to account for temporal colony variation.

2.6. Statistical Analysis

Data were analyzed using three-way Analysis of Variance (ANOVA) with colony state, colony hybrid, and larval origin as fixed factors. Colony identity was included as a random factor nested within hybrid type to account for colony-level variation. Normality and homogeneity of variance were verified using Shapiro-Wilk and Levene's tests, respectively. Post-hoc pairwise comparisons were conducted using Duncan's Multiple Range Test (DMRT) at $\alpha = 0.05$. Least Significant Difference (LSD) values were calculated for each factor. All statistical analyses were performed using SPSS version 26.0 (IBM Corp., Armonk, NY). Data are presented as mean ± standard error (SE).

3. Results

3.1. Queen Cell Acceptance Rates

3.1.1. Main Effects

Colony State Effect: Colony state exerted a significant main effect on acceptance rates ($F = 12.47$, $P = 0.005$). Queenless colonies demonstrated significantly higher mean acceptance rate (61.8 ± 2.5%) compared to queenright colonies (58.5 ± 3.3%; $LSD_{0.05} = 1.828$) (Table 1).

Colony Hybrid Effect: Colony hybrid also significantly influenced acceptance rates ($F = 31.82$, $P < 0.001$). Italian hybrid colonies exhibited superior performance (64.0 ± 1.9%) relative to Carniolan hybrid colonies (56.3 ± 2.2%; $LSD_{0.05} = 1.024$) (Table 1).

Larval Origin Effect: Larval genetic origin showed no significant effect on acceptance rates ($F = 0.14$, $P = 0.715$). Italian-origin larvae (60.5 ± 3.8%) and Carniolan-origin larvae (59.8 ± 2.1%) were accepted at statistically equivalent rates ($LSD_{0.05} = 1.108$) (Table 1).

3.1.2. Interaction Effects

Analysis revealed significant two-way interactions between colony state and colony hybrid ($F = 8.31$, $P = 0.016$), indicating that the advantage of Italian colonies was more pronounced under queenless conditions. No significant interactions involving larval origin were detected (all $P > 0.05$).

Table (1). Acceptance rates (% ± SE) of grafted queen cells as influenced by colony state, colony hybrid, and larval origin

Larval Origin	Queenright Colonies			Queenless Colonies			Overall Mean
	Italian	Carniolan	Mean	Italian	Carniolan	Mean	(by origin)
Italian	66.5	53.0	59.7±6.1	66.6	56.0	61.3±5.1	$60.5±3.8^{A}$
Carniolan	60.2	54.4	57.3±2.9	62.7	61.9	62.3±0.9	$59.8±2.1^{A}$
Overall Mean	63.4±3.8	53.7±0.7	$58.5±3.3^{B}$	64.7±2.8	59.0±4.2	$61.8±2.5^{A}$	60.2±2.1
Mean/colony hybrid			Italian $64.0±1.9^{A}$ | Carniolan $56.3±2.2^{B}$				

Within each main effect, means followed by different superscript letters differ significantly ($P < 0.05$, Duncan's test). LSD values: Colony State = 1.828; Colony Hybrid = 1.024; Larval Origin = 1.108.

3.2. Royal Jelly Production

3.2.1. Main Effects

Colony State Effect: The data presented in table (1) showed that the presence or absence of the queen significantly affected royal jelly yield per cell (F = 9.86, P = 0.010). Queenless colonies produced significantly more royal jelly (150.1 ± 3.2 mg/cell) compared to queenright colonies (143.7 ± 3.1 mg/cell; $LSD_{0.05}$ = 4.404) (Table 2).

Colony Hybrid Effect: No significant difference in royal jelly production was observed between Italian (147.7 ± 2.3 mg/cell) and Carniolan hybrid colonies (147.2 ± 2.8 mg/cell; F = 0.02, P = 0.893; $LSD_{0.05}$ = 6.135) (Table 2). However, these results were found to be heavily dependent on the colony queen state, indicating a strong interaction

Larval Origin Effect: Under queenless conditions, colonies grafted with Carniolan larvae yielded the highest amounts of RJ, particularly when housed in Carniolan hybrid colonies (156.9 mg), but when colonies were queenright, the total amount of RJ produced decreased to 142.6 mg/cup. Interestingly, under queenright conditions, Italian colonies grafted with Italian larvae produced more RJ (150.3 mg) than Carniolan origin larvae (141.1 mg) when housed in the same Italian colonies, suggesting that Italian colonies maintain better feeding activity even when a queen is present. However, in general, weight of the collected RJ did not appear to be significantly influenced by the genetic larval origin (F = 0.09, P = 0.771).

3.2.2. Interaction Effects

No significant two-way or three-way interactions were detected for royal jelly production (all P > 0.10), indicating that the effect of colony state was consistent across hybrid types and larval origins.

Table (2). Royal jelly production (mg/cell ± SE) as influenced by colony state, colony hybrid, and larval origin

Larval Origin	Queenright Colonies			Queenless Colonies			Overall Mean
	Italian	Carniolan	Mean	Italian	Carniolan	Mean	(by origin)
Italian	150.3	141.1	145.7±5.5	146.4	148.1	147.3±4.4	$146.5±3.1^{A}$
Carniolan	144.8	142.6	143.7±3.1	149.1	156.9	153.0±3.7	$148.4±2.5^{A}$
Overall Mean	147.6±3.9	141.9±1.1	$144.7±3.1^{B}$	147.8±1.9	152.5±6.2	$150.1±3.2^{A}$	147.4±2.5
(by hybrid)	$147.7±2.3^{A}$ | $147.2±2.8^{A}$						

Within each main effect, means followed by different superscript letters differ significantly (P < 0.05, Duncan's test). LSD values: Colony State = 4.404; Colony Hybrid = 6.135; Larval Origin = 3.207.

4. Discussion

4.1. Colony State as the Primary Determinant

This study demonstrates that colony state-specifically the presence or absence of a functional queen-constitutes the most influential factor governing both queen cell acceptance and royal jelly production efficiency. Queenless colonies exhibited significantly elevated acceptance rates (5.6% increase) and royal jelly yields (4.4% increase) relative to queenright counterparts, consistent with the emergency queen-rearing response documented in previous studies (**Pettis *et al*., 1998; Sahinler and Kaftanoglu, 1997 and Collins *et al*., 2012**).

The mechanistic basis for enhanced performance in queenless colonies likely involves multiple pheromonal and behavioral pathways. Queen mandibular pheromone (QMP) acts as a potent inhibitor of queen cell construction and worker ovarian development (**Pankiw *et al*., 1998 and Hoover *et al*., 2003**). Following queen removal, the rapid decline in QMP concentration releases workers from reproductive suppression, triggering an urgent colony-level response to rear replacement queens

(**Winston, 1987**). This emergency response manifests as: (i) increased nurse bee attentiveness to young larvae, (ii) enhanced hypopharyngeal gland activity and royal jelly secretion, and (iii) accelerated queen cell construction (**Free, 1987**).

Our findings support the widespread commercial practice of utilizing queenless "starter" colonies for initial graft acceptance, often followed by transfer to queenright "finisher" colonies for cell completion. However, the persistent advantage of queenless colonies in royal jelly production suggests that maintaining queenless conditions throughout the 72-hour harvest period may optimize yields, despite potential management challenges associated with prolonged queenlessness.

4.2. Genetic Background Effects: Differential Acceptance but Equivalent Provisioning

The superior acceptance rates observed in Italian hybrid colonies (64.0% vs. 56.3% in Carniolan hybrids) align with established behavioral differences between these subspecies. Italian bees (***A. m. ligustica***) are characterized by sustained brood production, reduced swarming tendency, and consistent maintenance of large worker populations (**Guzmán-Novoa *et al*., 2010**), traits that collectively enhance their suitability for artificial queen rearing systems. Previous comparative studies have similarly reported higher queen cell acceptance rates in Italian stocks relative to other European subspecies (**Kahya *et al*., 2008 and Cobey *et al*., 2013**).

In contrast, Carniolan bees (***A. m. carnica***), while exhibiting rapid spring buildup and exceptional gentleness, demonstrate more pronounced seasonal brood cycling and higher natural swarming propensity (**Rinderer, 1986**). These characteristics may reduce their responsiveness to artificial queen-rearing stimuli, particularly when colonies are not in an active swarming state. The significant colony state × colony hybrid interaction observed in acceptance rates suggests that the Italian advantage is most pronounced under queenless conditions, when emergency response pathways are maximally activated.

Notably, despite differential acceptance rates, Italian and Carniolan colonies produced statistically equivalent quantities of royal jelly per accepted cell (147.7 mg vs. 147.2 mg). This dissociation between acceptance behavior and provisioning intensity suggests that once queen cells are initiated and accepted, nurse bee feeding behavior is relatively uniform across genetic backgrounds. This finding contradicts earlier assumptions that high-acceptance genotypes would necessarily exhibit enhanced provisioning and supports the conclusion of **Santos *et al*., (2019)** that royal jelly yield is more strongly influenced by colony demographic structure and nutritional status than by genetic background per se.

4.3. Absence of Larval Origin Effects: Implications for Kin Recognition

The lack of significant larval origin effects on either acceptance rates or royal jelly production represents a key finding with both theoretical and practical implications. Despite documented kin recognition capabilities in honey bees (**Page and Erickson, 1986**), nurse workers in this study exhibited no detectable preference for conspecific versus allospecific larvae. Acceptance rates were statistically equivalent for Italian-origin (60.5%) and Carniolan-origin (59.8%) larvae, regardless of nurse bee genetic background.

This result corroborates earlier findings by **Woyke (1980)**, who reported minimal genetic discrimination during early larval acceptance phases. Several non-exclusive explanations may account for this pattern:

Superorganism-Level Selection: Colony-level imperatives may override individual kin preferences when queen replacement is urgently required (**Tarpy *et al*., 2004; Franks and Wenseleers, 2004**). The critical need to establish a new queen following queen loss may suppress fine-scale kin discrimination mechanisms that operate during normal colony maintenance.

Developmental Stage Limitations: Kin recognition in honey bees relies primarily on cuticular hydrocarbon profiles, which are poorly developed in newly-hatched larvae (**Page and Erickson, 1986**).

First-instar larvae (12-24 hours old) may lack sufficient chemical cues for reliable subspecies-level discrimination.

Dilution of Genetic Signatures: In commercial hybrid colonies, genetic heterogeneity within the worker population (resulting from queen polyandry) may reduce the salience of subspecies-level genetic differences relative to within-colony patriline variation.

Behavioral Plasticity: Nurse bees may exhibit behavioral plasticity that prioritizes functional queen rearing over genetic discrimination when confronted with artificial queen cells and young larvae requiring immediate provisioning.

From a practical standpoint, this finding is advantageous for commercial operations, as it permits the use of genetically diverse larval sources in specialized queen-rearing colonies without penalties in acceptance rates or provisioning quality. Beekeepers can strategically combine high-acceptance cell-builder stocks (e.g., Italian hybrids) with larvae from diverse genetic backgrounds to maximize production efficiency.

4.4. Production System Recommendations

Based on our findings, we propose the following evidence-based recommendations for commercial queen rearing and royal jelly production:

For Maximum Acceptance Rates:

- Utilize queenless starter colonies to exploit emergency response mechanisms
- Employ Italian hybrid colonies as cell builders, particularly when maximum acceptance is prioritized
- Larval source can be selected based on desired queen genetics without concern for acceptance penalties

For Maximum Royal Jelly Yields:

- Maintain queenless conditions throughout the 72-hour production cycle
- Either Italian or Carniolan colonies can be utilized, as genetic background does not significantly affect royal jelly quantity
- Focus management efforts on maintaining optimal colony strength, adequate protein nutrition, and high nurse bee populations rather than genetic selection

For Integrated Systems:

- A two-stage system combining queenless Italian colonies (for initial acceptance) with subsequent transfer to queenright colonies (for cell completion) may balance acceptance efficiency with colony stability
- When producing queens for specific genetic programs, larval source selection should prioritize desired breeding traits without concern for cross-fostering penalties

4.5. Study Limitations and Future Directions

Several limitations warrant acknowledgment. First, this study examined only initial acceptance (24 hours) and royal jelly production (72 hours) but did not assess long-term queen quality parameters (e.g., emergence rates, virgin queen weight, mating success, or reproductive performance). Subtle genetic discrimination effects could manifest in post-acceptance provisioning patterns or queen developmental outcomes not captured in our measurements.

Second, we examined only two subspecies hybrids under specific environmental conditions (Egyptian climate during nectar flow). Results may vary with different genetic stocks, geographical locations, or seasonal contexts.

Third, our analysis focused on quantitative royal jelly production but did not assess biochemical composition, which may differ based on colony genetics or state.

Future research should address: (1) post-acceptance queen quality metrics and long-term colony performance of queens reared in cross-fostering systems; (2) royal jelly composition analysis across genetic backgrounds and colony states; (3) comparative assessment of additional ***A. mellifera*** subspecies and their hybrids; (4) temporal dynamics of acceptance and provisioning throughout extended production cycles; and (5) economic optimization models integrating acceptance rates, royal jelly yields, and colony management costs.

5. Conclusions

This study provides systematic evidence that colony state and genetic background exert primary control over queen cell acceptance and royal jelly production, while larval genetic origin plays a negligible role. Queenless colonies and Italian hybrid colonies demonstrated superior performance in acceptance rates, whereas royal jelly production was influenced solely by colony state. The absence of larval origin effects indicates that nurse bees do not exhibit subspecies-level discrimination during emergency queen rearing, facilitating flexible breeding strategies in commercial operations.

These findings support the theoretical framework that superorganism-level imperatives override individual kin preferences during critical colony reproductive events. Practically, results suggest that beekeepers can optimize production systems by prioritizing colony state management and appropriate cell-builder stock selection while maintaining flexibility in larval source genetics. Further investigation into post-acceptance queen quality parameters and royal jelly compositional variation would enhance our understanding of the full implications of these genetic and physiological interactions.

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