

# Dietary supplementation with a molybdenum-based complex is associated with higher emergence weight in *Apis mellifera* queens under field conditions

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## ABSTRACT

The quality of the queen is a key factor in the performance of honeybee colonies. Yet the role of trace-element supplementation in queen rearing remains insufficiently documented. This study investigated whether dietary supplementation with the molybdenum-based complex abbreviated Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA affected queen-rearing traits in *Apis mellifera* under field conditions. Experiments were conducted in spring 2024 in two apiaries in western France. Supplemented colonies received sugar syrup containing Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA, whereas control colonies received the same syrup without supplementation. Queen emergence weight was assessed at both sites, and additional queen-rearing traits were measured at one site.

Three replicates were conducted at both sites, although one replicate at site 1 was excluded because of high mortality. After accounting for colony identity, site, and week effects using mixed-effects models, dietary supplementation with Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA was significantly associated with increased queen emergence weight. In contrast, no consistent treatment effect was detected for queen cell length, royal jelly production, or morphometric traits. These results provide preliminary evidence that molybdenum supplementation may influence queen developmental outcomes under field conditions and support further investigation of trace-element supplementation in honey bee queen rearing.

**Keywords:** Molybdenum, Honey bees, Queen rearing, Nutrition

## 1. INTRODUCTION

Honey bee colonies are exposed to multiple stressors, including pathogens, parasites, pesticides, environmental change, habitat alteration, and nutritional shortages, all of which can impair colony health and survival (Goulson et al., 2015; Vanbergen, 2014; Tsuruda et al., 2021; Lin et al., 2024; Steinhauer et al., 2018). In eusocial honey bees (*Apis mellifera*), caste differentiation depends strongly on larval rearing conditions, with nutrition playing a central role in queen development (Kamakura, 2011). Queen quality is a multifactorial concept that includes reproductive capacity, longevity, immune status, nutritional status, and interactions with workers (Margarita, 2020), and colony performance is closely linked to queen condition (Copeland et al., 2024; Holmes et al., 2023; Nelson & Gary, 1983; Rangel et al., 2013; Yu et al. 2023). In particular, larval diet, including the quantity and composition of royal jelly, is known to influence queen development (Slater et al., 2020; Pirk, 2018; Taha et al., 2025).

In this context, nutrition is an important determinant of colony resilience and queen production in apiculture (Lau et al., 2023; Tsuruda et al., 2021; Vaudo et al., 2015; De Souza et al., 2019; Fèvre, 2024). Honey bee nutritional requirements remain complex and incompletely understood, as they depend on a balance between macro- and micronutrients (Bonoan et al., 2018; Bonoan et al., 2017; Lau et al., 2023). Honey bees obtain essential nutrients from nectar and pollen, but the availability and diversity of these resources vary with season, weather, and floral environment (Vaudo et al., 2015; Tsuruda et al., 2021; Topal et al., 2022).

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To compensate for nutritional limitations, beekeepers commonly use supplemental feeding, most often in the form of sugar syrups or fondants, which can also serve as carriers for additional nutrients such as vitamins, proteins, sterols, or microbial supplements (Tsuruda et al., 2021; Jovanovic et al., 2021; Ricigliano et al., 2022; García-Vicente et al., 2023; García-Vicente et al., 2024; Pavlović et al., 2025; Bogaert et al., 2025).

By contrast, the role of minerals, and especially trace elements, in honey bee nutrition remains comparatively less documented, despite their essential physiological functions (Herbert, 1979; Zhang et al., 2015; Bonoan et al., 2018). Recent work has highlighted the potential interest of mineral supplementation for worker physiology, including hypopharyngeal gland development under laboratory conditions (Ghasemi et al., 2025). Among trace elements, molybdenum is of particular interest because it serves as a cofactor for several oxidoreductases involved in intermediary metabolism and redox regulation (Schwarz et al., 2009; Dow, 2017). Honey bees naturally contain molybdenum at low levels in the 0.2 to 0.5 ppm range (Benner et al., 2025; Fuior et al., 2025). In particular, Fuior et al. (2025) evidenced that Mo is found in the cuticle and in all tagma of the honey bees, especially in the head (brain, hypopharyngeal glands) and in the abdomen, but its role in honey bee health, its impact in honey bee nutrition and the benefits of molybdenum supplementation in apiculture and notably in queen rearing remain little or not explored.

Previous studies have shown that supplementing bees with the complex  $\text{Na}_2[\text{Mo}_2\text{O}_4(\text{EDTA})]$  (denoted hereafter Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA), both in the laboratory and under field conditions, leads to a significant increase in molybdenum levels in honeybees, associated with beneficial effects at the colony level, notably higher honey production and reduced winter mortality under specific experimental conditions (Fuior et al., 2025; Benito-Murcia et al., 2025). To our knowledge, the question of whether such supplementation can also influence characteristics related to queen rearing has not yet been investigated under real field conditions, and this aspect could provide further insights into the mode of action of this molecule.

The aim of the present study was therefore to assess whether dietary supplementation with Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA, delivered in a commercial sugar syrup, was associated with variation in queen-rearing traits in *Apis mellifera* under field conditions in two apiaries in western France. We examined royal jelly production, queen cell length, queen emergence weight, and selected morphometric traits. Because queen emergence weight is commonly used as an informative indicator of their developmental conditions and has been associated with their later reproductive performances (Hatjina et al., 2014; Amiri et al., 2017; Kahya et al., 2008), this parameter was considered alongside the other measured traits, without being treated as a comprehensive proxy for overall queen quality.

## 2. MATERIALS AND METHODS

### 2.1. Study sites

The study took place in two independent apiaries in two neighboring departments in the Nouvelle-Aquitaine region, in the West part of France, during the spring 2024. The first site was located in Lagord (lat: 46.208, long: -1.034, Charente-Maritime, France) and was used for experiments on royal jelly characteristics, queen cells sizes, morphological characteristics (queen head width, thorax width, wings length) and queen weights at emergence. The second site was located in Saint-Laurent-de-la-Salle (lat: 46.593, long: -0.938, Vendée, France) and was used for experiments on royal jelly characteristics and queen weights at emergence.

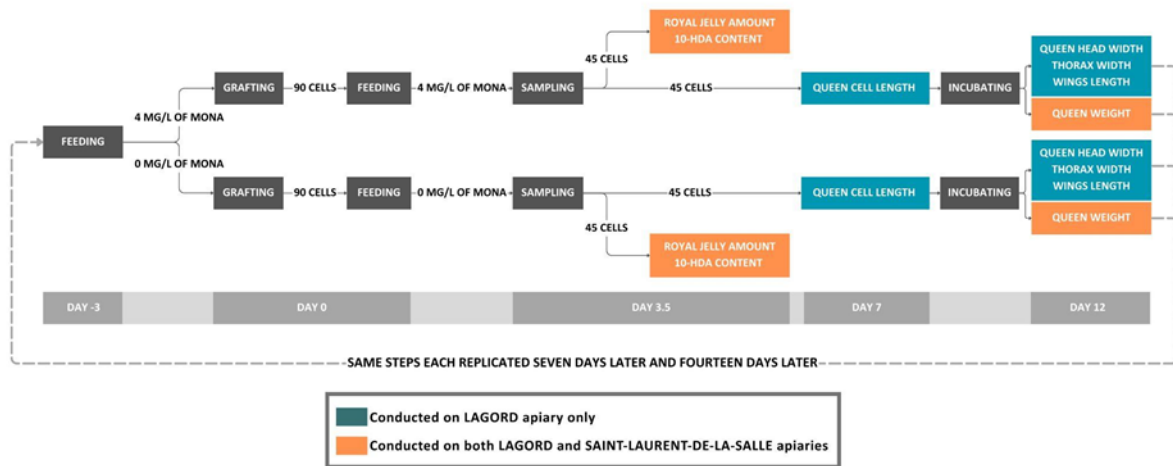
### 2.2. Feeding syrups composition

The control diet was composed of plain sugar syrup ('Apistar', ICKO Apiculture®). This syrup was composed of 34% of sucrose, 33% of fructose and 33% of glucose. For the supplemented syrup, the molybdenum-based complex Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA, was diluted in the syrup at a concentration of 4 mg/L (1.15 mgMo/L, 1.7 mgMo/kg with a density of the syrup equal to 1.46). The concentration of Mo was checked by ICP-MS method by laboratory LEAV, La Roche sur Yon (France). The complex was synthesized as previously described (Fuior et al 2022, 2025). Two liters of Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA provided 8 mg of the complex per colony.

### 2.3. Experimental design and measurements

At site 1 (Lagord), the experiment followed a 12-day queen-rearing protocol. Three colonies received either syrup supplemented with Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA while 3 colonies received the corresponding control syrup. Colonies were randomly assigned to the control or supplemented feeding condition. All grafted larvae originated from a single selected donor colony. For each feeding condition, three breeder colonies were prepared at the start of each replicate. The protocol was repeated three times, starting on 10, 17, and 24 June 2024, respectively, using the same breeder colonies across weeks. The third replicate at site 1 was excluded from analysis because high mortality in both groups resulted in an insufficient number of viable queens for meaningful comparison. The cause of this mortality could not be established.

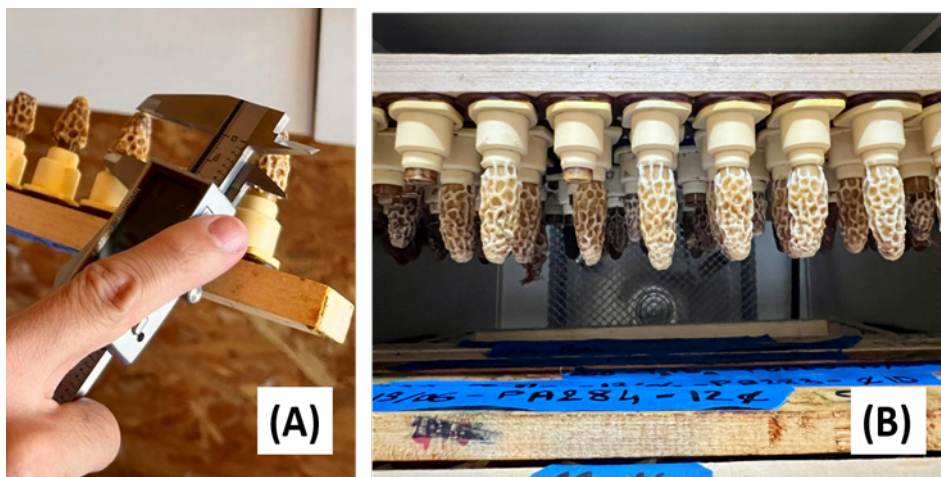
Three days before grafting (D-3), colonies were pre-fed with 2 L of syrup. On day 0 (D0), each breeder colony received 30 grafted larvae, resulting in 90 queen cells per feeding condition, and colonies were then fed again with 2 L of the corresponding syrup. At D+3.5, approximately 10 queen cells per hive and per feeding condition were sampled to quantify royal jelly production per cell, and a small amount of royal jelly was retained for 10-HDA analysis. At D+7, queen cell length was measured on the remaining cells using a caliper, after which the cells were placed in an incubator. At D+12, newly emerged queens were weighed using a precision balance (1 mg resolution), and morphometric traits (head width, thorax width, and wing length) were measured from scaled photographs using ImageJ. Morpho-



**Figure 1:** Experimental protocol scheme. Days are colored in gray above and below the principal scheme. Actions in the process are colored in black. Measurement types are colored in orange if conducted on both Lagord and Saint-Laurent-de-la-Salle apiaries and in blue if conducted only on Lagord apiary.

metric measurements were performed by a single operator blinded to feeding conditions.

At site 2 (Saint-Laurent-de-la-Salle), the same protocol was applied with 6 colonies, randomly divided into two groups of 3 for each modality, to assess royal jelly production and queen emergence weight. The experiment was conducted in three replicates starting on 14, 21, and 28 June 2024. All raw data are provided in Tables S1–S4 in the Supporting Information.



**Figure 2.** (A) Queen cells for the measurements of the royal cell length; (B) Queen cells in incubation.

#### 2.4. Analyses of the royal jelly

As an exploratory analysis, the 10-HDA content of royal jelly was assessed because this compound is a characteristic bioactive component of royal jelly (Genç & Aslan, 1999; Wang et al., 2016; Howe et al., 1985). To obtain sufficient material for HPLC analysis, royal jelly samples were pooled by feeding condition, following the analytical approach described by Kim and Lee (2010). One pooled sample per feeding condition was analysed by Intertek (Germany). Because no replicated analytical measurements were available at the treatment level, 10-HDA results were considered descriptive only and were not subjected to statistical comparison.

#### 2.5. Statistical analysis

Because the dietary treatment was applied at the colony level, colonies were considered the primary experimental units. To account for the hierarchical structure of the dataset and avoid pseudo-replication, the effects of treatment were analyzed using mixed-effects models.

For queen emergence weight, the following model was fitted:

$$\text{Weight} \sim \text{Treatment} + \text{Site} + \text{Week} + (1|\text{Colony})$$

where Treatment, Site and Week were included as fixed effects and Colony identity as a random effect (to account for repeated measurements performed on the same breeder colonies across experimental weeks).

For queen cell length, a mixed-effects model including Treatment and Week as fixed effects and Colony as a random

effect was fitted.

Morphometric traits (head width, thorax width and wing length) were analysed using similar mixed-effects models with Treatment and Week as fixed effects and Colony as a random effect.

Royal jelly production was considered exploratory because of the limited number of independent observations available at the colony level. Therefore, no inferential statistical analysis was performed and results are presented descriptively.

All analyses were performed in R (R Core Team, 2024) using mixed-effects modelling approaches (Mixed-effects models were fitted using the lme4 package and p-values were obtained using lmerTest).

### 3. RESULTS

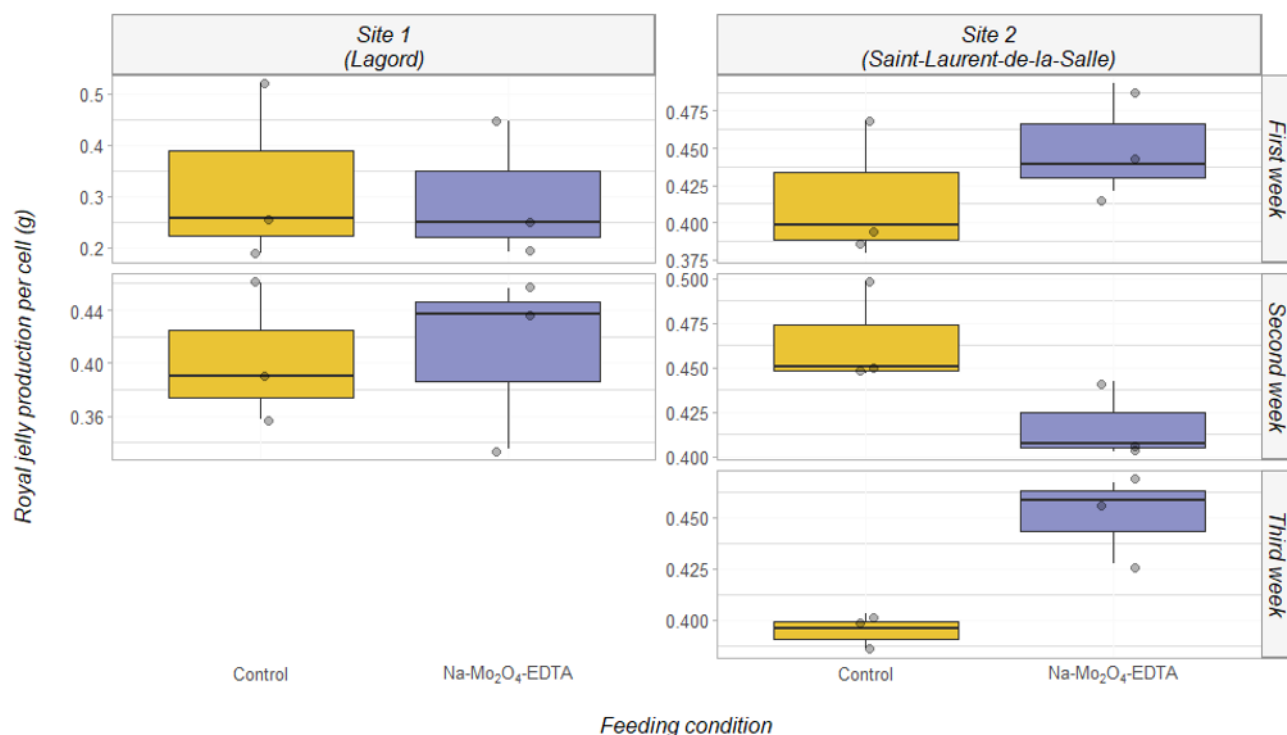
At site 1, results are reported for the first two experimental weeks only, as the third replicate was excluded because of high mortality and an insufficient number of viable queens for analysis ( $n = 6$  or less).

#### 3.1. Royal jelly production

Royal jelly production varied among weeks and sites, but no consistent pattern associated with dietary supplementation was observed (Figure 3).

Given the limited number of independent colony-level observations available for this parameter, royal jelly production was considered exploratory and no inferential statistical analyses were performed. Consequently, the results are presented descriptively only.

The pooled royal jelly sample obtained from supplemented colonies showed a slightly higher 10-HDA content (3.80%) than the pooled control sample (3.59%). Because these measurements were performed on pooled samples



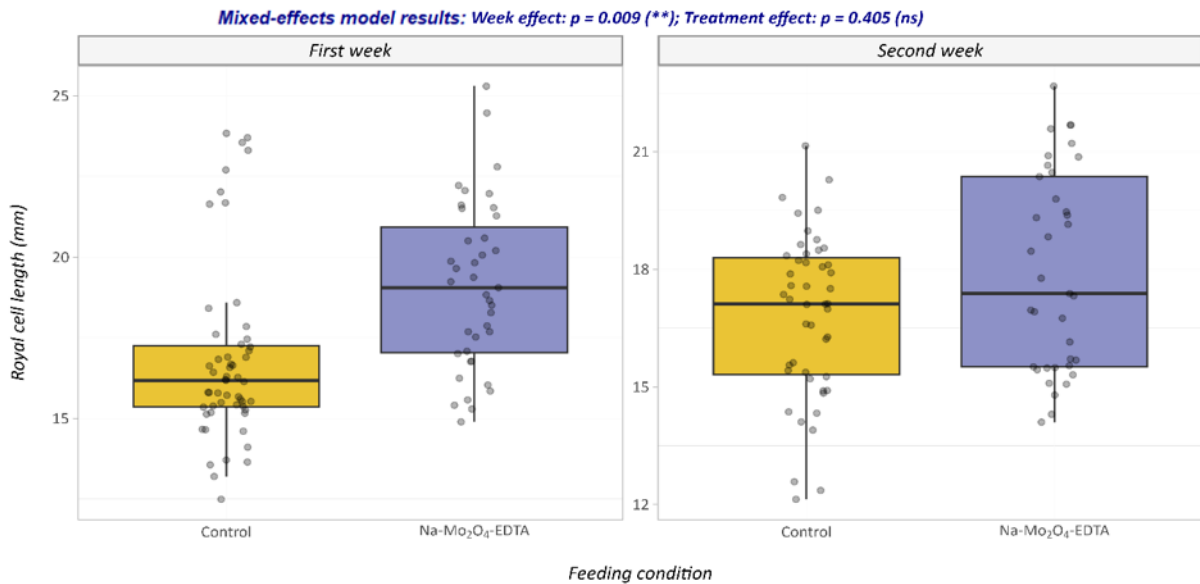
**Figure 3.** Royal jelly production per cell (g) according to feeding condition (“Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA” or “Control”), study site, and experimental week. Boxplots show the median, first and third quartiles, and whiskers extending to  $1.5 \times$  the interquartile range. Individual points represent colony-level observations. Given the limited number of independent observations available, these data are presented descriptively and were not subjected to inferential statistical testing.

without analytical replication, they should be considered descriptive only.

#### 3.2. Queen cell length

At site 1, Figure 4 shows queen cell length according to feeding condition, with raw data provided in Table S2 (SI). The mixed-effects model revealed a significant effect of week on queen cell length ( $p = 0.0009$ ), whereas no significant effect of dietary supplementation was detected ( $p = 0.405$ ).

Although queens reared in supplemented colonies tended to develop in slightly longer queen cells during some experimental replicates, this pattern was not consistent enough to support an overall treatment effect after accounting

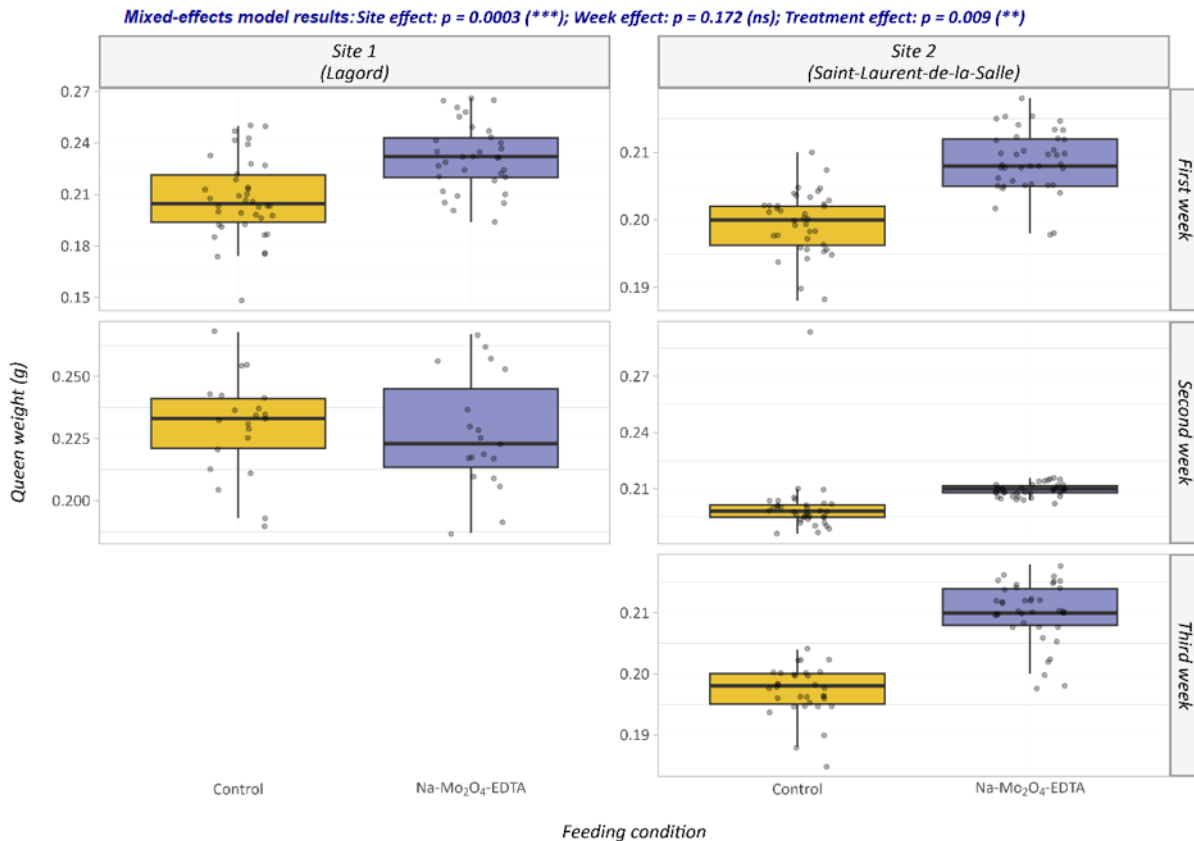


**Figure 4:** Queen cell length (mm) according to feeding condition (“Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA” or “Control”) and experimental week. Boxplots show the median, first and third quartiles, and whiskers extending to 1.5 × the interquartile range. Individual points represent measured queen cells. Results from the mixed-effects model are shown above the figure (Week effect:  $p = 0.009$ ; Treatment effect:  $p = 0.405$ ).

for colony-level variability.

### 3.3. Queen weight at emergence

The mixed-effects analysis revealed a significant effect of dietary supplementation on queen emergence weight (Treatment effect:  $p = 0.009$ ; Figure 5). Queens originating from colonies receiving Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA supplementation were consistently heavier than queens originating from control colonies across most experimental replicates. A strong site effect was also detected ( $p = 0.0001$ ), indicating substantial differences between the two apiaries. In contrast, the effect of experimental week was not significant ( $p = 0.172$ ). These results indicate that the positive association between Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA supplementation and queen emergence weight remained significant after accounting



**Figure 5:** Queen emergence weight (g) according to feeding condition (“Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA” or “Control”), study site, and experimental week. Boxplots show the median, first and third quartiles, and whiskers extending to 1.5 × the interquartile range. Individual points represent emerging queens. Results from the mixed-effects model are shown above the figure (Site effect:  $p = 0.0003$ ; Week effect:  $p = 0.172$ ; Treatment effect:  $p = 0.009$ ).

for colony-level variability and the hierarchical structure of the experiment.

### 3.4. Morphometric parameters

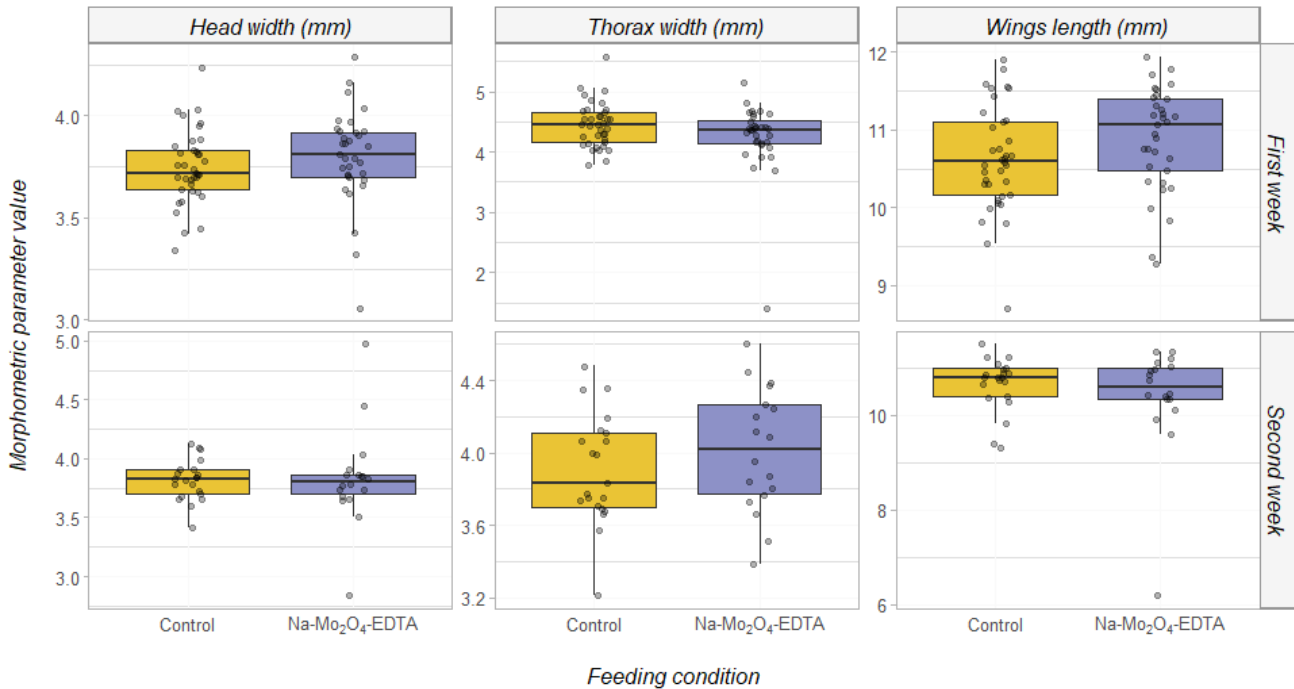
Mixed-effects analyses did not detect any significant effect of dietary supplementation on head width ( $p = 0.333$ ), thorax width ( $p = 0.249$ ) or wing length ( $p = 0.789$ ) (Figure 6).

A significant week effect was detected only for thorax width ( $p < 0.0001$ ), whereas no significant week effect was observed for head width ( $p = 0.497$ ) or wing length ( $p = 0.176$ ).

Overall, the morphometric data do not support a consistent effect of Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA supplementation on structural queen morphology.

*Treatment effect (Mixed-effects model results): Head width  $p = 0.333$  (ns); Thorax width  $p = 0.249$  (ns); Wings length  $p = 0.789$  (ns)*

*Week effect (Mixed-effects model results): Head width  $p = 0.497$  (ns); Thorax width  $p < 0.0001$  (\*\*\*) ; Wings length  $p = 0.176$  (ns)*



**Figure 6:** Head width (mm), thorax width (mm), and wing length (mm) of queens according to feeding condition (“Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA” or “Control”) and experimental week. Boxplots show the median, first and third quartiles, and whiskers extending to 1.5 × the interquartile range. Individual points represent measured queens. Results from the mixed-effects models are shown above each panel. No significant treatment effect was detected for head width ( $p = 0.333$ ), thorax width ( $p = 0.249$ ), or wing length ( $p = 0.789$ ). A significant week effect was detected only for thorax width ( $p < 0.0001$ ).

## 4. DISCUSSION

The present study investigated whether dietary supplementation of honey bee colonies with the molybdenum-based complex Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA was associated with variation in queen-rearing traits under field conditions. After accounting for the hierarchical structure of the experiment through mixed-effects modelling, the principal finding was that queens originating from supplemented colonies exhibited a significantly higher emergence weight than queens originating from control colonies. In contrast, no overall treatment effect was detected for queen cell length, royal jelly production, or the morphometric traits measured.

The increase in queen emergence weight is of particular interest because emergence weight is commonly considered an informative indicator of queen developmental conditions and has been associated with subsequent reproductive performance, sperm storage capacity, and longevity (Amiri et al., 2017; Hatjina et al., 2014; Kahya et al., 2008). Under the conditions tested here, queens produced by colonies receiving Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA supplementation were consistently heavier across sites and experimental replicates. Importantly, this association remained significant after accounting for colony identity, site effects, and temporal variation, suggesting that the observed difference was not solely attributable to colony-specific characteristics or environmental heterogeneity. Nevertheless, emergence weight alone cannot be considered a comprehensive measure of queen quality, and the present results should not be interpreted as evidence that all aspects of queen performance are improved by supplementation.

A major contribution of the present work is the use of a statistical framework that explicitly accounts for the experimental design. Because supplementation was applied at the colony level rather than at the level of individual queens, colonies represent the true experimental units. The mixed-effects models used in the analyses account for this structure and reduce the risk of pseudo-replication. Using this model, the treatment effect on queen emergence weight appears significant. This outcome strengthens confidence that the observed pattern reflects a genuine biological signal rather than an artefact arising from non-independent observations.

The mechanisms through which molybdenum supplementation may influence queen development remain unclear. Molybdenum is an essential trace element involved in several oxidoreductase systems and metabolic pathways (Schwarz et al., 2009; Dow, 2017; Marelja et al., 2018). Previous studies have shown that supplementation with Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA can increase molybdenum concentrations in honey bee tissues and may improve physiological parameters related to oxidative balance and colony performance (Fuior et al., 2025; Benito-Murcia et al., 2025). It is therefore conceivable that enhanced nutritional or physiological status of nurse bees could indirectly affect larval development and queen growth. However, the present study was not designed to investigate physiological mechanisms, and any causal link between molybdenum supplementation, nurse-bee physiology, royal jelly composition, and queen development remains hypothetical.

In contrast to queen emergence weight, no overall treatment effect was detected for queen cell length. Although some individual experimental replicates suggested longer queen cells in supplemented colonies, this pattern was not consistent across the study. Queen cell size has previously been associated with developmental and morphometric characteristics of queens (Mattiello et al., 2022; Wu et al., 2018), but the present results do not provide evidence that Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA supplementation systematically influences this parameter. The significant week effect observed for queen cell length indicates that temporal factors may have contributed more strongly to variation than dietary supplementation.

Similarly, no significant treatment effect was detected for head width, thorax width, or wing length. Morphometric traits are known to exhibit substantial biological variability and may be sensitive to measurement error despite careful standardization (Fox et al., 2020; Fruciano, 2016). The absence of detectable differences in these parameters suggests that any influence of supplementation on structural morphology is either limited or smaller than the effect observed for emergence weight. Additional studies involving larger numbers of colonies and complementary measurements of reproductive anatomy would be required to determine whether molybdenum supplementation influences other dimensions of queen quality.

Royal jelly production and 10-HDA content were evaluated as exploratory variables. No consistent pattern associated with supplementation was observed for royal jelly production across sites and weeks. Furthermore, 10-HDA measurements were performed on pooled samples and therefore do not allow statistical inference. Although previous work has suggested that molybdenum supplementation may influence hypopharyngeal gland physiology (Fuior et al., 2025), the present data are insufficient to determine whether changes in royal jelly characteristics contributed to the differences observed in queen emergence weight.

A significant site effect was detected for queen emergence weight, highlighting the importance of environmental context in queen-rearing experiments. Differences in floral resource availability, weather conditions, colony strength, brood dynamics, and overall nutritional status are known to influence queen development and colony performance (Vaudo et al., 2015; Lau et al., 2023; Tsuruda et al., 2021). Such factors likely contributed to the variability observed between apiaries and may partly explain why the magnitude of the treatment effect differed among replicates. Consequently, caution is warranted when extrapolating these findings beyond the specific conditions investigated here.

Overall, the present results provide preliminary field evidence that dietary supplementation with Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA may positively influence queen emergence weight in honey bees. However, because the study involved a limited number of colonies and was conducted during a single season, further experiments across multiple environmental conditions and years will be necessary to assess the reproducibility of this effect and to determine whether the increase in emergence weight translates into measurable improvements in queen performance, colony productivity, or colony survival.

## 5. CONCLUSION

Under the conditions tested in two field apiaries, dietary supplementation with the molybdenum-based complex Na-Mo<sub>2</sub>O<sub>4</sub>-EDTA remained significantly associated with higher queen emergence weight in *Apis mellifera*, after accounting for colony-level variability whereas effects on royal jelly production, queen cell length, and morphometric traits were limited or inconsistent across sites and experimental weeks. These results suggest that molybdenum supplementation may influence some queen-rearing outcomes under field conditions, but they do not support a general improvement across all measured traits.

The present study therefore provides preliminary field evidence that trace-element supplementation deserves further investigation in honey bee queen rearing. Additional studies are needed to assess the reproducibility of the effect across colonies, seasons, and environmental conditions, to deeply investigate the impact on the quality of royal jelly (notably biochemical or nutritional profiling), and to clarify whether the observed association with queen emergence weight translates into measurable differences in subsequent queen performance and colony development.

## AUTHOR CONTRIBUTIONS

Conceptualization, P.C., B.P. and S.F.; Methodology, A.M., P.C., B.H., R.A., B.P. and S.F.; Formal Analysis, P.C.; Writing-Original Draft Preparation, A.M., P.C. and S.F.; Writing-Review and Editing, P.C., A.M., B.P. and S.F. All authors have read and agreed to the published version of the manuscript.

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## DATA AVAILABILITY

Raw data can be found online as supplementary data from the present publication.

## CONFLICT OF INTEREST

SF is linked to a patent about the technology used in this study (European Patent EP4185594B1 delivered on 4th December 2024) and consultant for Oligofeed SAS (as SFConsulting), which cofunded this work and aims to commercialize the complex for the beekeeping industry. The authors declare these interests in the interest of full transparency and affirm that the reported findings are presented objectively and without bias.

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## DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

Statement: The authors did not use generative AI technologies for preparation of this work. The author takes full responsibility for the publication's content.

## SUPPORTING INFORMATION

Table S1 contains raw data concerning the royal jelly production on sites 1 and 2; Table S2 contains raw data about the cell length measured on site 1; Table S3 contains raw data about queen weight, head width, thorax width and wings length measured on site 1 for weeks 1 and 2; Table S4 contains raw data about queen weight measured on site 2 for weeks 1-3 (Cochard et al., 2026).

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