

REDUCING RELIANCE ON ARTIFICIAL DIETS: BIOECONOMIC NUTRITIONAL STRATEGIES FOR MAINTAINING *SPODOPTERA LITTORALIS* (BOISD.) (LEPIDOPTERA: NOCTUIDAE) COLONIES

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Abstract

The Egyptian cotton leafworm, *Spodoptera littoralis*, is a widely distributed polyphagous species that attacks several economically important host plants. Laboratory colonies of this species have been vital for pest management research, with more recent applications emerging in the context of sustainable food systems. Current reliance on artificial diets for colony maintenance is expensive and environmentally unsustainable. In this study, alternative bioeconomic dietary strategies are investigated using dandelion leaves (D) and unsold market vegetables (beetroot and potato mix, BP) as substitutes for the standard artificial diet (S). Over five generations, key life history parameters, including larval duration, survival, final instar weight, pupation success, adult emergence, and fecundity, were monitored under controlled laboratory conditions. The results showed that larvae fed on D exhibited the shortest development time, highest survival rates, and superior fecundity compared to those reared on other diets. The BP diet supported performance comparable to the artificial diet. These findings show that alternative diets can sustain *S. littoralis* colonies, enhance certain biological traits, and offer a cost-effective, sustainable approach to insect farming.

KEY WORDS: dandelion, beetroot, potato, cost-effectiveness

Introduction

Many of the landmark achievements in modern biology owe a great deal to the use of insect laboratory colonies. These model organisms, relatively easy to rear, cost-effective, and rapidly reproducing, have firmly established themselves in both fundamental and applied sciences (Francuski & Beukeboom, 2020). By controlling farming

parameters, researchers can maintain desired traits across generations, ensuring both the replicability of experiments and the generation of robust biological insights (Dickie *et al.*, 2019; Madau *et al.*, 2020). Over the course of the twentieth century, the field expanded through standardized rearing practices, while the adoption of unified nomenclature for strains and stocks, along with informative colony designations, improved transparency and cross-lab comparability (Cadinu *et al.*, 2020). Today, Lepidoptera are commonly bred as model organisms to investigate questions in genetics, endocrinology, and physiology, as well as for use in bioreactor and pharmacological research (Ahlawat & Sharma, 2023; Alizadeh *et al.*, 2024). They also play an integral role in developing pest management programs and biological control strategies (Kolliopoulou & Swevers, 2014). While the silkworm, *Bombyx mori* (Linnaeus, 1758), has also long been a focus of research into alternative protein sources, and is easily studied in controlled lab conditions, efforts to systematically introduce other lepidopteran species for this purpose have been relatively limited. Most available data on edible lepidopteran insects, aside from *B. mori*, still come from wild-caught specimens or processed goods available through Asian and African markets (Mbata, 2002; Siddiqui *et al.*, 2023) rather than well-established colonies. As the demand for sustainable protein sources grows, expanding the scope of lepidopteran rearing to include additional species and diets may offer new opportunities for improved food security, but also deeper insights into their biology and ecology. In general, insects are highly valued, since they offer significant nutritional benefits, such as high levels of protein, lipids, essential amino acids, and valuable micronutrients (Rumpold & Schlüter, 2013). Insect farming requires less water, energy, and land, while producing fewer greenhouse gas emissions than livestock farming, which is known for its negative impact on the environment (van Huis *et al.*, 2013; Kouřimská & Adámková, 2016). Moreover, insects exhibit high feed conversion efficiency, effectively transforming what they eat into protein (Feng *et al.*, 2017). Although nutritional needs are highly species-specific, some can even be raised on manure waste (Varelas, 2019). However, EU legislation strictly limits the use of domestic waste and livestock manure because of the potential risks they pose to human and animal health (Cappellozza *et al.*, 2019).

Entomophagy has been practiced for thousands of years in many parts of the world, especially among ethnic groups in Africa, Asia, and South America, where more than 2 billion people consume insects as part of their diet (Yi *et al.*, 2010; van Huis *et al.*, 2013; Yen, 2015). The most commonly used insects include beetles, caterpillars, bees, wasps, ants, grasshoppers, locusts, crickets, and termites (Baiano, 2020). Among lepidopterans, two Saturniidae species, *Gonimbrasia belina* Westwood, 1849, and *Cirina forda* (Westwood, 1849) are the most widely consumed and important insect food sources in Africa, also serving as significant income generators (Nemadodzi *et al.*, 2023). A comprehensive list of edible caterpillars in Mexico can be found in Ramos-Elorduy *et al.* (2011).

The edible insect sector presents vast opportunities for exploring lepidopteran species, especially those with a long history of traditional use in different regions. However, this comes with a unique set of challenges. While the ability to easily modify an insect's bioactive and nutritional profile through diet is a clear advantage, enabling researchers to tailor feeding regimes for specific nutritional outcomes, this same flexibility can make colony maintenance more challenging. The order Lepidoptera underwent the largest known herbivory radiation in evolutionary history, so it is unsurprising that modern caterpillar species feed on foliage and other plant parts (Powell *et al.*, 1998). The degree of specialization varies widely among species; some require large quantities of fresh plant food for successful farming, while others can thrive on artificial or semi-artificial diets. For example, farming *B. mori* requires a constant inflow of fresh mulberry leaves (Ayandokun & Alamu, 2020), while the fall armyworm *Spodoptera frugiperda* (J. E. Smith, 1797) accepts a range of corn-based diets (Ge *et al.*, 2022). Like many other pestilential noctuid caterpillars that lay eggs in clusters and thus rely on a life history strategy that emphasizes high offspring numbers, congeners of this species also exhibit satisfactory development on semi-artificial diets composed of kidney beans or chickpeas, potato mash, and cereal flour (Gupta *et al.*, 2005; Pinto *et al.*, 2019).

Among lepidopteran species with potential for laboratory rearing and sustainable insect-based protein production, the Egyptian cotton leafworm, *Spodoptera littoralis* (Boisduval, 1833), stands out as a widely distributed, generalist, polyphagous species that feeds on economically important plant species from more than 40 plant families (Sorour *et al.*, 2011; Mokbel & Huesien, 2020; Hemmati *et al.*, 2022). Although it is not commonly consumed as food and has not been thoroughly investigated in this context, many studies focus on its use in insect-based feed for animals (Sayed *et al.*, 2019). For this purpose, caterpillars are mostly reared under laboratory conditions and fed on artificial diets (Cabello *et al.*, 1984; El-Awady *et al.*, 2009).

Other studies involving *S. littoralis* have focused on nutritional responses and developmental traits by rearing wild-type populations on a variety of host plant species. These evaluations were conducted to evaluate the caterpillar's defoliation potential and feeding impact in pest management research. Although life table studies are commonly employed to assess population stability, predict outbreaks, understand the dynamics of invasive species, and develop population models (Carey, 1993, 2001; Vargas *et al.*, 1997; Haghani *et al.*, 2006), they can also serve as an effective screening tool. By evaluating insect performance across different diets, analyses of developmental parameters can identify which feeding strategies are feasible and practical for further development, serving as a preliminary step before conducting detailed chemical profiling.

Dietary conditions affect both the population growth rate and the survival of insects at all life stages (Velasco & Walter, 1993; Makkar *et al.*, 2015). Previous studies have shown that *S. littoralis* exhibits variations in survival, fecundity, and developmental rates (Makkar *et al.*, 2015) depending on the host plant species, with different crop plant hybrids also affecting larval nutritional performance (Alekar *et al.*, 2024). As with other generalist noctuid diets, formulations for this species always typically include a gelling agent (agar), a starch source (such as a variety of beans, crushed host plant leaves, cereal flour etc.), yeast for activation, and preservatives (such as ascorbic acid and methyl benzoate) (Anderson *et al.*, 1995; Sorour *et al.*, 2011). Comparing species performance across studies is challenging due to misreporting or underreporting of the source egg batch and laboratory protocols, as well as geographic variations in climate and plant composition, seasonal effects, and differences in how life history traits are measured.

Given today's emphasis on more sustainable solutions in research and development, and especially when an insect colony holds potential for future product development, whether via direct use of larvae, pupae, or through targeted compound extraction, artificial and semi-artificial diets may not represent the most suitable long-term option. Since *S. littoralis* has already demonstrated excellent performance on both natural and processed food sources, we explored whether maintenance protocols could be adapted to include some underutilized food inputs. Specifically, we focused on dandelion leaves and unspoiled beetroot and potato remnants from local markets, produce typically discarded for superficial defects rather than poor quality. Several studies have shown that these vegetable byproducts retain valuable nutrients and can serve as effective components of insect feed, enhancing both sustainability and diet diversity (Angulo *et al.*, 2012; Bakshi *et al.*, 2016; Tedesco *et al.*, 2021; Fan *et al.*, 2023; Khanal *et al.*, 2024; Stoica *et al.*, 2025). To achieve this, we have tested three feeding treatments for *S. littoralis* larvae: standard artificial diet, fresh dandelion leaves, and unsold market vegetables (potato and beetroot), and compared their effects on key biological characteristics.

Materials and Methods

A closed colony of *Spodoptera littoralis* was established in 2023, with the egg batches obtained from Andermatt AG, Switzerland. Insect stock is maintained in the laboratory of the Faculty of Sciences and Mathematics, Department of Biology and Ecology, University of Niš, Serbia, at room temperature, a 16:8 LD photoperiod, humidity levels ranging from 35-50% in the lab, and 50-70% in the rearing containers. Larvae were reared on

a starch-based artificial diet following the formulation of Shorey and Hale (1965), with modifications: dry beans were replaced with instant mashed potato flakes and wheat germ.

In this experiment, we collected life history data of F7-F11th spring/summer generations across three dietary groups: artificial diet (S), dandelion leaves (D) and a 1:1 mixture of beetroot and potato slices (BP) (Fig. 1). Dandelion leaves were periodically harvested near the city of Niš, Serbia, disinfected in 2.5% bleach solution and stored in a refrigerator until use. The vegetables (white 'Kennebec' potatoes and 'Kestrel' beetroots) were sourced twice a month from small, local producers using low-intensity farming methods. The vendors set aside cosmetically imperfect specimens, which are typically avoided by customers. Upon receipt, the vegetables were stored in a dark, cool environment until use. At the beginning of each experimental generation, 100 newly hatched L₁ larvae were carefully transferred with a fine brush into perforated transparent plastic containers measuring 35 × 25 × 15 cm. For each dietary group, three replicates were established and maintained across all five generations. Offspring from each replicate were used to initiate the next generation within the same dietary treatment and replicate, maintained under identical experimental conditions. To ensure optimal ventilation, a hole was cut in the lid of each container and then covered with nylon mesh. Throughout the experimental period, hygiene was maintained by regularly removing excrement, leftover food, or any deceased caterpillars. Larval mortality was recorded daily, and fresh food was provided *ad libitum* until pre-pupal wandering behavior was observed. Before this stage, the weight of all L₆ larvae was recorded. To facilitate pupation, containers were filled to one-third of their volume with sterilized soil, and a moistened piece of cotton was added to maintain optimal humidity. The number of unsuccessful pupae (larval-pupal intermediates) was also documented, along with the duration of the pupal stage. Adult emergence was recorded daily, and newly emerged adults were transferred to breeding containers, where they were provided with a 10% sucrose solution on cotton wool for nutrition. A zigzag-folded paper was placed at the bottom of each container to increase the surface area available for oviposition. The number of eggs laid per cluster was counted daily until the adults' death. This experiment was repeated across five generations under identical laboratory conditions, with the same parameters monitored as in the initial experiment. Mating was restricted to individuals from the same dietary group, though not necessarily from the same replicate. Adult individuals were paired without deliberate selection for traits such as size or emergence time, thereby reducing the potential for selection bias.

Data for all biological traits recorded across the consecutive generations, each reared on one of the three diets (artificial diet – S, dandelion leaves – D, and beetroot/potato mix – BP), were collected, organized, and checked for normality. Statistical comparisons were performed within each generation to determine whether these parameters differed significantly among the three diet treatments. One-way analysis of variance (ANOVA) was employed for each generation, with diet treated as the fixed factor, using a two-tailed test. Post-hoc comparisons were then carried out using Tukey's HSD test to determine which diet groups differed significantly within each generation. Mean values were presented with standard deviations, and groups not sharing the same superscript letter were considered statistically significantly different at $P < 0.05$. Statistical analyses were conducted in Python (v3.11) using the PyCharm IDE. Data processing was performed using pandas (v2.2.3), and statistical tests were conducted with SciPy (v1.10.1).

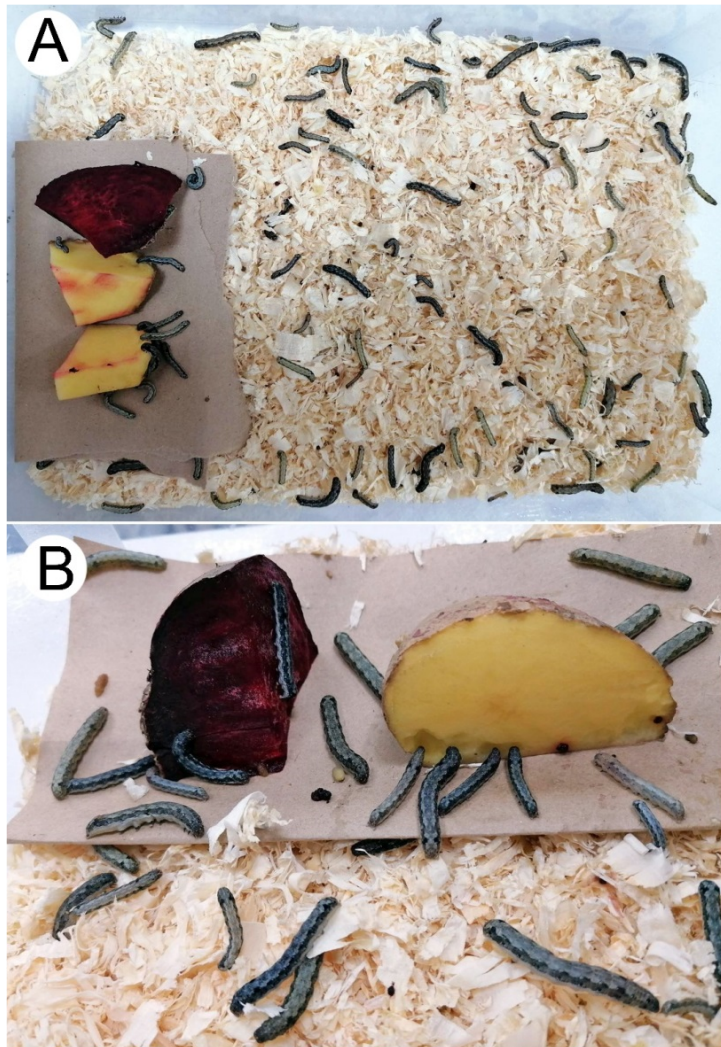


Figure 1. Closed colony of *Spodoptera littoralis* feeding on the potato/beetroot diet: A – overview of the population in a growing box; B – close-up of feeding behavior.

Results and Discussion

The results in Table I show that *Spodoptera littoralis* colonies can be successfully maintained on locally sourced alternative diets – dandelion leaves (D) and a beetroot-potato mix (BP) – while achieving performance in certain life history characteristics that is comparable to, or even exceeds, that of the standard artificial diet (S).

Table I. Life history traits of *Spodoptera littoralis* across five consecutive spring/summer generations reared on three diets: standard laboratory diet (S), dandelion leaves (D), and beetroot–potato mix (BP). Values are presented as mean \pm standard deviation (SD), except for larval-pupal intermediates, which are shown as cumulative percentages per generation.

	Diet	Larval stage duration (days)	Larval survival rate (%)	L6 weight (g)	Larval-pupal intermediates (cumulative %)	Pupal stage duration (days)	Emergence rate (%)	Fecundity (number of eggs per cluster)
F1	S	20.45 \pm 2.26	21.0 \pm 1.0	1.01 \pm 0.1	9.09	10.53 \pm 1.71	85.17 \pm 5.07	179.44 \pm 43.12
	D	16.79 \pm 1.65	51.67 \pm 5.69 ^s	1.14 \pm 0.17	8.51	8.95 \pm 2.39	93.36 \pm 2.26	218.85 \pm 55.59
	BP	18.88 \pm 1.34	35.67 \pm 10.26	1.09 \pm 0.14	0	11.0 \pm 1.39	94.70 \pm 3.06	210.0 \pm 44.72
F2	S	18.68 \pm 2.78	29.33 \pm 2.08 ^a	1.03 \pm 0.11	7.41	10.34 \pm 1.66	95.40 \pm 2.52	185.88 \pm 41.05
	D	16.19 \pm 1.61	35.33 \pm 3.21 ^b	1.23 \pm 0.72	2.56	8.91 \pm 2.32	92.87 \pm 1.80	247.39 \pm 42.34
	BP	19.0 \pm 1.33	33.33 \pm 7.64	1.12 \pm 0.11	8.1	10.97 \pm 1.42	94.61 \pm 3.25	212.78 \pm 40.56
F3	S	19.85 \pm 2.5	33.33 \pm 3.06 ^a	1.07 \pm 0.09	0	10.5 \pm 1.68	95.25 \pm 1.50	188.16 \pm 36.37
	D	16.32 \pm 1.86	39.67 \pm 1.53 ^b	1.22 \pm 0.1	2.56	8.96 \pm 1.34	93.81 \pm 1.03	249.44 \pm 42.49
	BP	19.13 \pm 1.3	34.33 \pm 0.58	1.18 \pm 0.64	5.13	11.06 \pm 2.44	91.24 \pm 2.55	228.0 \pm 28.83
F4	S	19.56 \pm 2.46	35.67 \pm 5.5	1.04 \pm 0.1	6.14	10.45 \pm 1.7	96.63 \pm 2.54	175.38 \pm 37.33
	D	16.31 \pm 1.82	41.67 \pm 2.52	1.14 \pm 0.16	5.26	9.04 \pm 1.30	92.39 \pm 1.13	218.0 \pm 61.78
	BP	19.48 \pm 1.34	39.0 \pm 9.54	1.08 \pm 0.13	5.13	11.91 \pm 0.88	94.30 \pm 2.06	207.06 \pm 45.52
F5	S	19.29 \pm 2.57	28.0 \pm 1.7 ^a	1.04 \pm 0.91	9.09	10.93 \pm 1.7	97.64 \pm 0.58	173.5 \pm 42.02
	D	16.2 \pm 1.96	44.0 \pm 5.57 ^b	1.15 \pm 0.15	6.14	8.90 \pm 0.36	92.31 \pm 3.17	237.5 \pm 56.04
	BP	18.95 \pm 1.32	36.33 \pm 2.08	1.09 \pm 0.13	0	11.05 \pm 1.43	95.63 \pm 2.11	217.27 \pm 38.49
Overall performance								
	S	19.57 \pm 0.66	29.47 \pm 5.64	1.04 \pm 0.02	6.35 \pm 3.76	10.55 \pm 0.22	94.02 \pm 5.04	180.47 \pm 6.40
	D	16.36 \pm 0.25	42.47 \pm 6.05	1.18 \pm 0.05	5.01 \pm 2.53	8.95 \pm 0.06	92.95 \pm 0.64	234.24 \pm 15.13
	BP	19.09 \pm 0.24	35.73 \pm 2.17	1.11 \pm 0.04	3.67 \pm 3.56	11.20 \pm 0.40	94.10 \pm 1.67	215.02 \pm 8.17

*Superscript letters (a, b) indicate statistically significant differences among diet groups within the same generation ($P < 0.05$). Superscripts are shown only for traits and generations where differences were statistically significant.

Variability for larval-pupal intermediates was not recorded due to their low occurrence and the non-central nature of the trait.

Larval stage duration was consistently shortest in the dandelion group (D), ranging from 16.2 to 16.79 days across generations, while the standard diet (S) group exhibited the longest duration, between 19.29 and 20.45 days. The beetroot-potato group (BP) showed intermediate values (18.88–19.48 days). The shorter development time on the D diet suggests that fresh leaves offer a readily digestible food source, likely owing to their balanced nutrient and water content. The artificial diet (S), although standardized, may contain suboptimal texture or palatability, potentially contributing to slower development. Prolonged development times when using standard/artificial diets are not unusual in lepidopteran insects (Ojeda-Avila *et al.*, 2003; Su *et al.*, 2021). The data suggest a potential trend towards fresh food sources, though this did not reach statistical significance.

Similarly, the D group consistently exhibited the highest survival rates (51.67 \pm 5.69% in F1 and 44.0 \pm 5.57% in F5) while the standard diet group showed significantly lower survival rates, dropping to 21.0 \pm 1.0% in F1 and 28.0 \pm 1.7% in F5. The BP group exhibited survival rates closer to those of the D group, 39.0 \pm 9.54% in F4. Although statistically significant differences were only observed between the S and D groups in three generations, the overall trends in mean values across generations consistently favor the alternative diets.

Larval weights at the final instar reflected the overall nutritional adequacy of each diet. The D group tended to achieve the highest mean L₆ weights (1.14–1.23 g) across generations, indicating efficient nutrient utilization, likely due to the unprocessed nature of the diet. In contrast, L₆ weights in the S group remained consistently

lower, ranging from 1.01 to 1.07 g. The BP group also performed well, maintaining intermediate L6 weights between 1.08 and 1.18 g across generations. A notable observation, rarely recorded in life history studies, was the occurrence of larval-pupal intermediates, individuals exhibiting incomplete metamorphosis, which may reflect suboptimal physiological states or diet-induced stress. While the D group exhibited low but consistent rates of intermediates (e.g., 2.56–6.14%), the BP group had no intermediates in several generations. In contrast, the S group showed the highest overall intermediate rates, including 9.09% in F1 and 6.14–9.09% in later generations. Variability was not recorded or analyzed due to the low and inconsistent occurrence of intermediates across replicates.

Although statistical differences in pupal stage duration were not detected, a biologically consistent trend emerged: the D group generally exhibited shorter durations (8.90 to 9.04 days) compared to the BP (10.97–11.91 days) and S (10.45–10.93 days) groups. A shorter pupal stage suggests more efficient energy accumulation during larval stages. Emergence rates were uniformly high across all diet groups, with the S group reaching particularly high values in some generations (e.g., $97.64 \pm 0.58\%$ in F5). Although these differences were not statistically significant, the consistent emergence rates across diets indicate a stable pattern of adult emergence under all tested conditions.

Fecundity, measured as the number of eggs per cluster, was particularly high in insects reared on the D diet, which yielded the highest values across generations (249.44 ± 42.49 eggs in F3 and 237.5 ± 56.04 eggs in F5). The BP group also maintained high fecundity of approximately 210 to 228 eggs per cluster, generally outperforming that of the S diet. These findings indicate biologically meaningful differences in reproductive potential, even without statistical significance. Notably, the S group exhibited the lowest values, especially in later generations (173.5 ± 42.02 eggs in F5), suggesting a potential decline in performance over time.

The cumulative analysis of growth and reproductive traits across all five generations reinforces the trends observed within individual generations. In terms of adaptation dynamics, the D group consistently showed the shortest larval stage duration (16.36 ± 0.25 days), along with the highest survival rates ($42.47 \pm 6.05\%$) and fecundity (234.24 ± 15.13 eggs per cluster). The BP group demonstrated intermediate but reliable performance, with larval survival rates of $35.73 \pm 2.17\%$ and fecundity of 215.02 ± 8.17 eggs per cluster. Larval-pupal intermediates were lowest in the BP group ($3.67 \pm 3.56\%$) compared to the D ($5.01 \pm 2.53\%$) and S diets ($6.35 \pm 3.76\%$), suggesting a smoother developmental transition. The cumulative findings confirm that both alternative diets can successfully sustain *S. littoralis* colonies over multiple generations. Dandelion leaves emerge as the most favorable option for rapid development and higher reproductive output, while the beetroot-potato mix provides benefits in terms of developmental stability.

In line with previous studies and considering the native-range climate of *S. littoralis*, both alternative food sources produced expected outcomes, particularly in terms of developmental period and larval weight. Fecundity comparisons across studies are complicated by differing measurement methods; here, we report eggs per cluster, whereas others typically use eggs per female, per cluster, or per day (Mohamed *et al.*, 2019; Hemmati *et al.*, 2022; El-Refaie *et al.*, 2024). Although larval survival rates may seem low, especially compared to commonly farmed insects, this pattern is typical of noctuid species with high-fecundity reproductive strategies, where the large number of offspring compensates for lower individual survival (Du Plessis *et al.*, 2020).

The results from this study challenge the conventional reliance on artificial diets for maintaining lepidopteran colonies, especially when rearing generalist species. Beyond estimating the detrimental impact of caterpillars on certain cultivated and commercially important plants, both dandelion leaves and the beetroot-potato combination proved to be adequate alternative substrates that supported performance. The dandelion diet outperformed across most life history traits, including larval development time, survival, and fecundity, making it a solid candidate for further exploration. The BP diet, though slightly less efficient, yielded comparable

outcomes. Although only larval duration showed statistically significant differences, the findings are still informative, as consistent biological trends were observed across five generations, indicating clear directions for future research.

From a practical perspective, using these locally sourced food supplies reduces costs and minimizes dependence on rigid formulations, which is relevant for both laboratory and insect-farming operations during non-experimental maintenance phases or in regions with limited access to artificial diets. Further investigations into the nutrient composition, digestibility, and microbial contributions of these diets could provide insights not only into their mechanisms of success but also into their impact on the nutritional profile of the larvae.

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СМАЊЕЊЕ ЗАВИСНОСТИ ОД ВЕШТАЧКЕ ХРАНЕ: БИОЕКОНОМСКЕ СТРАТЕГИЈЕ ИСХРАНЕ ЗА ОДРЖАВАЊЕ КОЛОНИЈА *SPODOPTERA LITTORALIS* (BOISD.) (LEPIDOPTERA: NOCTUIDAE)

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Извод

Spodoptera littoralis, је широко распрострањена полифагна врста која напада више економски значајних биљака домаћина. Лабораторијске колоније ове врсте од кључног су значаја за истраживања у области сузбијања штеточина, а у новије време све више налазе примену у контексту одрживих система исхране. Тренутно ослањање на вештачке дијете за одржавање колонија је скупо и еколошки неодрживо. У овом истраживању испитиване су алтернативне биоекономске стратегије исхране употребом лишћа маслачка (D) и непродатог поврћа (мешавина цвекле и кромпира, BP) као замене за стандардну вештачку дијету (S). Током пет генерација, у контролисаним лабораторијским условима праћени су кључни параметри животног циклуса, укључујући трајање ларвеног стадијума, преживљавање, масу у последњем ларвеном ступњу, успешност улуткавања, еклозија имага и плодност. Резултати су показали да су ларве храњене D дијетом имале најкраће време развоја, највише стопе преживљавања и највећу плодност у поређењу са онима узгајаним на другим дијетама. BP дијета је подржавала перформансе сличне вештачкој дијети. Ови налази показују да алтернативне дијете могу одржати колоније *S. littoralis*, побољшати одређене биолошке особине и понудити исплатив, одржив приступ гајењу инсеката.

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