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Juvenile hormone-mediated accelerated post-flight recovery of ovarian development in *Loxostege sticticalis* (Lepidoptera: Crambidae)

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Abstract

The beet webworm *Loxostege sticticalis* (Lepidoptera: Crambidae) is a transcontinental migratory pest whose population outbreaks are driven by the coordination of migration and reproduction through the interplay of internal and external factors. This study reveals that prolonged flight in sexually immature adults induces two key post-flight responses: (1) increased feeding behavior and (2) flight muscle histolysis, characterized by ultrastructural reorganization of myofibrils and mitochondrial degeneration. These processes collectively redirect metabolic resources (lipids, glycogen, and amino acids) toward ovarian development. Concomitantly, flight accelerates juvenile hormone (JH) biosynthesis, which activates the JH receptor methoprene-tolerant (Met) and its downstream effector Krüppel-homolog 1. This signaling cascade upregulates vitellogenin expression and promotes yolk deposition. Crucially, RNA interference-mediated knockdown of *Met* disrupts ovarian development, suppresses fecundity, and abolishes flight-induced reproductive benefits, thereby establishing the necessity of this pathway. Together, these integrated mechanisms accelerate ovarian maturation and synchronize oviposition, effectively resolving the flight-reproduction trade-off by repurposing nutrients derived from flight muscles for vitellogenesis. Our findings elucidate key adaptive mechanisms underlying insect migration, identifying JH signaling and muscle remodeling as critical targets for disrupting life-history strategies and suppressing pest populations.

KEYWORDS

energy allocation, flight muscle histolysis, flight-reproduction trade-off, juvenile hormone signaling, *Loxostege sticticalis*

1 | INTRODUCTION

Insect migration represents a critical life-history strategy for adapting to seasonal and spatial heterogeneity in habitats.[1] This capacity enables transgenerational population redistribution and resurgence across generations. As an energetically demanding process, migration imposes significant physiological constraints, particularly on concurrent reproduction.[2] The classical 'oogenesis-flight syndrome' posits a trade-off, with

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energy preferentially allocated to flight musculature during migration, leading to delayed ovarian development or reduced fecundity.[3] However, evidence indicates that the reproductive impact of flight extends beyond simple suppression. Despite the initial energetic cost of sustained flight, post-migratory insects in diverse taxa—including *Melanoplus sanguinipes*,[4] *Aphis fabae*,[5] *Spodoptera exigua*,[6] *Cnaphalocrocis medinalis*,[7] and *Loxostege sticticalis*[8]—often exhibit uncompromised or even enhanced reproductive output.

The regulation of flight-enhanced reproduction involves the integration of environmental cues with endocrine signaling. Juvenile hormone (JH) serves as a central regulator in this process.[9] For instance, in *Mythimna separata*, flight stimulates the corpus allatum via neuropeptides, promoting allatotropin and suppressing allatostatin to activate JH synthesis.[10] Concomitantly, flight mobilizes carbohydrates and lipid reserves, leading to substantial substrate depletion.[11] This depletion drives a compensatory post-flight feeding response to replenish energy stores, a behavior observed in long-winged crickets.[12] Given the inherent survival-reproduction trade-off under nutritional limitation,[13] such energetic replenishment is critical for subsequent reproductive investment.[14] The reallocation of energy reserves can follow distinct pathways: in *M. separata*, triglycerides (TAGs) are redirected from flight muscles to ovaries at the cost of flight capacity,[8] whereas post-migratory *C. medinalis* utilizes retained glycogen and triacylglyceride pools to directly fuel oogenesis.[15]

Flight muscles serve as a critical nexus for reproductive energy redistribution in insects. Experimental ablation in *Pyrrhocoris apterus* demonstrates that histolysis of flight musculature enhances ovarian protein content and follicular development.[16,17] *C. medinalis* females maintain elevated glycogen reserves during muscular histolysis to support reproductive demands.[18] In *Gryllus bimaculatus*, the decline in flight capacity during ovarian maturation coincides with the progressive depletion of proteins, lipids, and carbohydrates from the flight muscles.[19] This process is accompanied by reduced mitochondrial oxidative capacity and accelerated histolysis prior to oogenesis initiation in long-winged crickets.[20]

Endocrine-mediated energy allocation governs life-history transitions in migratory insects. JH operates as the principal regulatory node: basal JH levels stimulate migratory behavior, whereas elevated titers activate Methoprene-tolerant and Krüppel-homolog 1 (Met/Kr-h1) signaling to initiate vitellogenin (Vg) biosynthesis and ovarian maturation.[21,22] Migratory locusts exemplify the coupling of enhanced JH secretion with reproduction.[23] In *M. separata*, precocious flight elevates hemolymph JH titer, accelerating oogenesis and shortening pre-oviposition intervals while depleting flight-essential TAGs.[24] Nutritional-JH crosstalk coordinates metabolic partitioning, as evidenced by *M. separata* prioritizing fecundity over flight persistence through lipid reserve reallocation.[25,26] JH further modulates flight muscle histolysis in orthopterans[27,28] and *Solenopsis invicta*, where corpus allatum excision prevents muscle histolysis, which can be reversibly rescued by JH administration.[29] Molecular analyses confirm JH stimulates Vg synthesis in the fat body, facilitating oocyte maturation through receptor-mediated endocytosis.[22,30,31] For black cutworm (*Agrotis ipsilon*), flight-induced upregulation of the JH acid methyltransferase gene elevates JH synthesis.[32] Functional validation through *Met* RNA interference (RNAi) confirms its indispensable role in lipid homeostasis and ovarian development in the migratory locust.[30,33]

The beet webworm, *Loxostege sticticalis* (Lepidoptera: Crambidae), is a transcontinental migratory pest whose adaptive strategy involves seasonal dispersal across Eurasian–North American ranges (36°–53°N) to avoid climatic extremes.[34,35] Although flight activity at 3 days old for 12 h is known to shorten the pre-oviposition period and enhances oviposition synchrony in this species,[34] the underlying regulatory mechanisms remain unclear. Based on evidence of flight-enhanced reproduction in other migratory insects, we proposed that flight accelerates reproductive development in *L. sticticalis* through a dual mechanism: by enhancing post-flight feeding and by inducing JH-mediated histolysis of flight muscles followed by nutrient reallocation. Through analysis of the *Met*/*Kr-h1* pathway, we demonstrate flight-driven hyperphagia and muscular histolysis jointly augment reserves of protein, TAG, and glycogen. Concurrent elevation of JH triggers *Met*/*Kr-h1*-mediated vitellogenesis, synergistically accelerating ovarian maturation and reproductive synchrony after migration. These findings establish an integrative framework linking extrinsic nutritional and mechanical inputs with intrinsic endocrine-metabolic networks in flight-optimized reproductive strategies.

2 | MATERIALS AND METHODS

2.1 | Insect rearing

L. sticticalis colonies were established from field-collected specimens in Hebei Province, China (41.73°N, 114.45°E). As this species is neither categorized as endangered nor protected, no special permits were required for specimen collection. Prior to experimentation, the insects were continuously reared in laboratory conditions for multiple consecutive generations. Larvae were maintained at a density of 10 individuals per bottle[36] and fed fresh seedlings of *Chenopodium album* L. (lamb's quarters). Mature larvae were transferred to sterile sandy soil (10 cm depth, ~10% moisture) for cocoon formation and pupation. Emerged adults were provided with a 10% (w/v) glucose solution, which was

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replenished daily. Throughout all developmental stages, the insects were maintained under controlled environmental parameters: temperature at 22 ± 1°C, relative humidity (RH) at 70% ± 5%, and a photoperiod of 16L:8D (light:dark).

2.2 | Flight assay and mating experiments

Unmated females (3-day-old) were tethered to a computerized flight mill (Jadoco Industry and Trade Co., Ltd.) by attaching a plastic harness (0.4 cm in length) to the back of the thoracico-abdominal junction with cyanoacrylate adhesive (502 adhesive). Prior to tethering, individuals were briefly anesthetized with diethyl ether (Sigma-Aldrich, USA) to remove thoracic scales and minimize handling stress. Flight assays were conducted in darkness (22 ± 1°C, 70% ± 5% RH) for 12 h (19:00–07:00) to align with nocturnal migratory activity. Age-matched untethered adults served as non-flight controls.[34] Immediately post-flight, flight females and non-flight controls were individually paired with age-synchronized males (maintained under a 16:8 L:D photoperiod, at 22 ± 1°C) in 200-mL transparent mating chambers. A minimum of 30 replicate pairs were established per treatment group. During flight treatment of the experimental *L. sticticalis* adults, the control group was subjected to starvation for the same duration. Pre-oviposition period was recorded daily, and egg masses were collected at 24-h intervals for fecundity analysis. Eggs were incubated at 75% RH until eclosion (larval hatching). Spermatophores were quantified by dissecting female bursae copulatrices in 0.1 M phosphate-buffered saline (PBS, pH 7.4) under a stereomicroscope (1× magnification), and were obtained using digital image analysis (Image-Pro Plus v6.0).

2.3 | Anatomy of the flight muscles and ovaries

Thoracic and abdominal samples from female adults were collected during specific post-flight intervals for comparative analysis. Thoracic specimens (0–3 days post-flight) were dehydrated in a laboratory oven (Shanghai Senxin Laboratory Instruments Co., Ltd.) at 55°C for 15 h. After drying, the dorsolongitudinal muscles were surgically isolated from the dorsal integument using microdissection needles, and the lateral dorsoventral muscles were removed according to established protocols.[8] Tissue dry mass was determined using an analytical balance (Mettler Toledo) with 0.01 mg precision; all values are expressed in milligrams (mg). For abdominal dissections (0–2 days post-flight), ovaries were first extracted into physiological saline. After carefully removing adipose tissue with micro-forceps, key morphological parameters of the ovarioles (basal diameter and length) were recorded under a stereomicroscopic examination (Leica). Ovarian developmental stages were classified as previously described[37] using the four-stage system illustrated in Supporting Information S1: Figure S1.

All procedures included non-flight female *L. sticticalis* as controls, following the same measurement protocols. For all groups, tissue dissection and collection were completed within 4 h after flight treatment.

2.4 | Preparation of flight muscle samples and electron microscopy

Following the flight experiments, dorsolongitudinal muscles were excised from the mesothorax at 0, 1, and 2 days post-flight. The dissection protocol followed the previously described methods,[38] using five adult specimens per timepoint, equally divided into transverse and longitudinal sectioning groups. Excised muscle tissues were fixed in 2.5% (v/v) glutaraldehyde in 0.1 M cacodylate buffer (pH 7.2) for 24 h. After removing the fixative, samples were rinsed with phosphate buffer (pH 7.3) and post-fixed in 1% osmium tetroxide for 1–2 h. This was followed by rinsing with phosphate buffer, stepwise dehydration through an ethanol series, clearance with acetone, and embedding in epoxy resin, which was polymerized overnight at 70°C. Ultra-thin sections (300–500 Å thickness) were cut using a Leica EM UC6 ultramicrotome, double-stained with uranyl acetate and lead citrate, and examined under a transmission electron microscope (Hitachi HT-7800). Imaging parameters were set as outlined by Chen et al.[39]

2.5 | Microscopic analysis of flight muscles

Fibril diameter in flight muscles was quantified as the maximum axis length of elliptical or polygonal cross-sectional profiles. Sarcomere length in longitudinal sections was measured as the linear distance between adjacent Z-discs. All dimensional data were obtained from calibrated electron micrographs containing embedded scale markers. Volumetric proportions of subcellular components were calculated using stereological analysis.

2.6 | Measurement of feeding intake

To quantify post-flight glucose feeding in *L. sticticalis* adults, intake was measured at 0.25, 0.5, 0.75, and 1 day after flight. The fluorescent glucose analog 2-[*N*-(7-nitrobenz-2-oxa-1,3-diazol-4-yl)amino]-2-deoxy-D-glucose (2-NBDG; excitation/emission: 467/542 nm) was

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used as a tracer. Experimental and control groups ($n \geq 5$ adults per group with the 1:1 sex ratio) were kept in 200-mL containers with continuous access to freshly prepared 400 μM 2-NBDG solution, which was replaced every 30 min. After feeding, samples were processed as follows: mechanical disruption (20 s), homogenization in 200 μL PBS (20 s), dilution with 800 μL PBS, and centrifugation (12,000 × g, 4°C, 2 min). The supernatant was heat-denatured (100°C, 10 min), mixed with an equal volume of chloroform, and centrifuged again. Fluorescence intensity was measured on a Hitachi F-7000 spectrofluorometer (excitation/emission: 467/536 nm; 96-well plate format) using 150 μL aliquots. Glucose uptake per μg body weight was calculated using a standard curve.

2.7 | Determination of energy reserves (triglycerides and glycogen), protein content, and ADP/ATP ratio

Energy metabolism was assessed in the thoracic and abdominal tissues of 3-day-old female *L. sticticalis* 0–3 days post a 12-h flight, using age-matched non-flight females as controls. Dissected tissues were flash-frozen in liquid nitrogen and stored at −80°C. TAG content was quantified with a GPO-PAP enzymatic colorimetric assay kit (Nanjing Jiancheng Bioengineering Institute), with absorbance measured at 546 nm.[15] Glycogen content was determined via the anthrone-sulfuric acid method using dextran as the standard (absorbance at 620 nm).[18] Total protein concentration was measured using a BCA assay with BSA standards (absorbance at 562 nm).[40] For ADP/ATP ratio analysis, tissues were dry-homogenized, lysed in PBS, and centrifuged. Ratios were determined using a luminescence-based assay kit (Vigorous Biotechnology, Beijing) according to the manufacturer's protocol. Briefly, lysates were mixed with the assay buffer and specific enzymes; luminescence readings taken before and after ADP conversion were used to calculate the ratio.

2.8 | JH quantification

JH I and JH II titers were measured using commercial enzyme-linked immunosorbent assay (ELISA) kits following the manufacturer's instructions. Each isoform was assayed with a separate kit, employing hormone-specific capture antibodies pre-coated on individual microplates (JH-I-specific for JH I; JH-II-specific for JH II). Samples and standards were added, followed by incubation with the corresponding HRP-conjugated detection antibody and extensive washing. Color was developed with TMB substrate; the resulting blue intensity was proportional to hormone concentration. Absorbance was recorded at 450 nm for quantification. The limit of detection (LOD) for both isoforms was <1.0 pg/mL, with intra-assay coefficients of variation (CV) < 10%. Three independent biological replicates were analyzed, each with triplicate technical replicates.[41]

2.9 | Real-time quantitative PCR (RT-qPCR)

To analyze the effects of flight on the expression of JH-pathway genes, specific tissues (head, thorax, fat body, and ovary) were dissected from adult females in each treatment group, flash-frozen, and stored at −80°C. Each biological replicate consisted of a pooled sample of tissues from 10 individuals, with four such replicates prepared for each group. Total RNA was extracted from all samples, and first-strand cDNA was synthesized from 1 μg of RNA using the PrimeScript 1st Strand cDNA Synthesis Kit (Takara Bio, Shiga, Japan) according to the protocol. Quantitative real-time PCR was performed with gene-specific primers on a Bio-Rad CFX96 system using TB Green Premix Ex Taq II (Tli RNaseH Plus) (Takara Bio). The cycling conditions were as follows: initial denaturation at 95°C for 30 s, 40 cycles of 95°C for 5 s and 60°C for 30 s, followed by melt curve analysis. Each sample was run in quadruplicate technical replicates. Relative expression levels of target genes were normalized to two reference genes (*eIF* and *18S* RNA) using the $2^{-\Delta\Delta CT}$ method.[42] Primers used for RT-qPCR can be found in Supporting Information S1: Table S1. Reference genes were selected as described by Tian et al.[43]

2.10 | RNA interference

Gene-specific siRNA targeting *Met* (*si-Met*; 40 μM) and non-targeting control siRNA (si-NC) were chemically synthesized by Tsingke Biotechnology Co., Ltd. (Beijing, China). Using a Nanoject III programmable microinjector, 2.0 ± 0.1 μL of siRNA solution was injected into the intersegmental membrane between abdominal segments 2 and 3 of 1-day-old adults under diethyl ether anesthesia. RNAi efficacy was validated by RT-qPCR using a Bio-Rad CFX96 system. After RNAi treatment, adults were subjected to a 12-h tethered flight (19:00–07:00) in darkness on a JR-01 flight mill system (Jiaduo Science & Technology Co. Ltd.) under the same photoperiod (16L:8D), temperature (22 ± 1°C), and humidity (70% ± 5% RH) conditions as their rearing conditions. Ovaries were then dissected and staged for developmental progression. Ovariole diameter and length were measured, and developmental stages were statistically compared. In parallel,

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key reproductive parameters—including the pre-oviposition period and fecundity—were recorded. The sequence of *si-Met* can be found in Supporting Information S1: Table S1.

2.11 | Statistical analysis

Data are presented as mean ± standard error (SE). Two-group comparisons used Student's *t*-tests (two-tailed), whereas multiple comparisons were analyzed by one-way ANOVA with Tukey's honestly significant difference with post-hoc test. Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3 | RESULTS

3.1 | Flight enhances nutrient acquisition and energy reallocation

Flight stimulated feeding in *L. sticticalis* adults, facilitating the rapid replenishment of energy reserves consumed during flight and reallocating energy toward reproductive processes to accelerate ovarian development. 2-NBDG labeling revealed significantly higher glucose intake in flown adults at 0.75 days post-flight compared to controls, with a non-significant sustained elevation thereafter (Figure 1A). Dynamic metabolic shifts were observed: thoracic TAGs decreased significantly by day 3 post-flight, whereas abdominal TAGs showed significant depletion on days 0–1, recover to control levels by day 2, and declining again on day 3 (Figure 1B,C). Thoracic glycogen levels dropped sharply immediately after flight but gradually rebounded, surpassing control levels by day 3. Concurrently, abdominal glycogen decreased significantly at flight termination before stabilizing (Figure 1D,E). Flight triggered enhanced oxidative phosphorylation in the abdomen, as indicated by elevated ADP/ATP ratios. Specifically, thoracic ratios rose significantly at day 3, moreover, abdominal ratios remained significantly higher than the controls during days 1–2 (Figure 1F,G). Additionally, thoracic protein content in the post-flight adults was significantly higher than that in the controls on day 1 after flight, and abdominal protein content was significantly elevated 1–3 days post flight (Figure 1H,I).

3.2 | Flight promotes flight muscle histolysis and ovarian development to shorten pre-oviposition period

Post-flight physiology in *L. sticticalis* was characterized by rapid yet transient flight muscle hypertrophy followed by histolysis. On one hand, flight adults developed more robust flight muscles compared to controls. At day 1 post-flight, the dry weight of flight muscles was significantly higher (Figure 2A). Myofibril diameter exceeded that of the controls on both day 0 and day 1 (Figure 2B), and sarcomere length was significantly greater immediately following the cessation of flight (Figure 2C). On the other hand, although flight muscle dry weight remained elevated relative to controls, the difference became non-significant thereafter (Figure 2A). Concurrently, myofibril diameter showed no significant difference from controls by day 2 post-flight (Figure 2B). Moreover, sarcomere length became significantly shorter than that of the controls at 1–2 days post-flight (Figure 2C). The volume fraction of myofibrils was also significantly lower in flight adults from day 0 to day 2 (Figure 2D). Ultrastructural analysis by scanning electron microscopy revealed myofilament breakage in transverse sections, manifested as significantly more blank gaps within the myofilaments in flight insects (Figure 2F); longitudinal sections displayed looser inter-filament connections compared to controls (Figure 2G). These structural changes coincided with mitochondrial histolysis, evidenced by a significant reduction in mitochondrial volume fraction (Figure 2E), confirming accelerated flight-muscle histolysis.

Ovarian morphological analysis confirmed accelerated development in flight adults. At day 0 post-flight, ovarian tubule diameter and length were significantly smaller in flight groups. However, by days 1–2, these parameters showed no significant differences from controls (Figure 3A–C). This accelerated development led to an increased proportion of Stage III ovaries by post-flight day 2, further enhancing the synchronization of ovarian development (Figure 3D), and significantly reducing the pre-oviposition period (Supporting Information S1: Table S2). This rapid maturation paralleled elevated abdominal protein levels at days 1–3 post-flight (Figure 1H,I), underscoring the critical role of protein allocation in ovarian development. Notably, the muscle-histolysis phase aligned temporally with rapid ovarian maturation documented in morphological assessments (Figure 3B,C), with ovarian development accelerated in parallel with flight muscle breakdown.

3.3 | Flight elevates JH titers and activates the Met/Kr-h1 pathway

The JH titer in *L. sticticalis* adults was determined following flight treatment. Post-flight adults exhibited significantly higher JH I titers compared to controls on days 0 and 2, whereas JH II showed no significant differences (Figure 4A,B). Meanwhile, the expression levels of JH-related *Met* and *Kr-h1* were determined in different tissues of *L. sticticalis* adults. The *Met* expression in head of post-flight adults displayed no significant differences compared to that of controls

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(Figure 4C), whereas thoracic *Met* was upregulated on days 0 and 1 with significant differences (Figure 4E). The expression of *Met* in fat body of post-flight adults was downregulated on day 0 compared to that of controls, showed no difference on day 1, but was significantly upregulated on day 2 (Figure 4G). Moreover, ovarian *Met* was significantly elevated throughout days 0–2 post flight (Figure 4I). Head *Kr-h1* increased significantly post flight across days 0–2 (Figure 4D). Thoracic *Kr-h1* rose on day 0, but declined on day 1 with no difference on day 2 (Figure 4F). The relative expression of *Kr-h1* in fat body was also increased significantly at all timepoints in post-flight adults, similar to that in the head (Figure 4H). Additionally, ovarian *Kr-h1* showed significant elevations on days 0 and 2 (Figure 4J). Furthermore, ovarian *Vg* expression significantly increased on days 1 and 2, though no changes were observed on day 0 (Figure 4K). Flight increases JH titers in *L. sticticalis* adults and elevates the expression of JH-related *Met* and *Kr-h1* genes in multiple tissues (head, thorax, fat body, and ovary), which presumably enhances ovarian *Vg* expression via the Met/Kr-h1 signaling pathway.

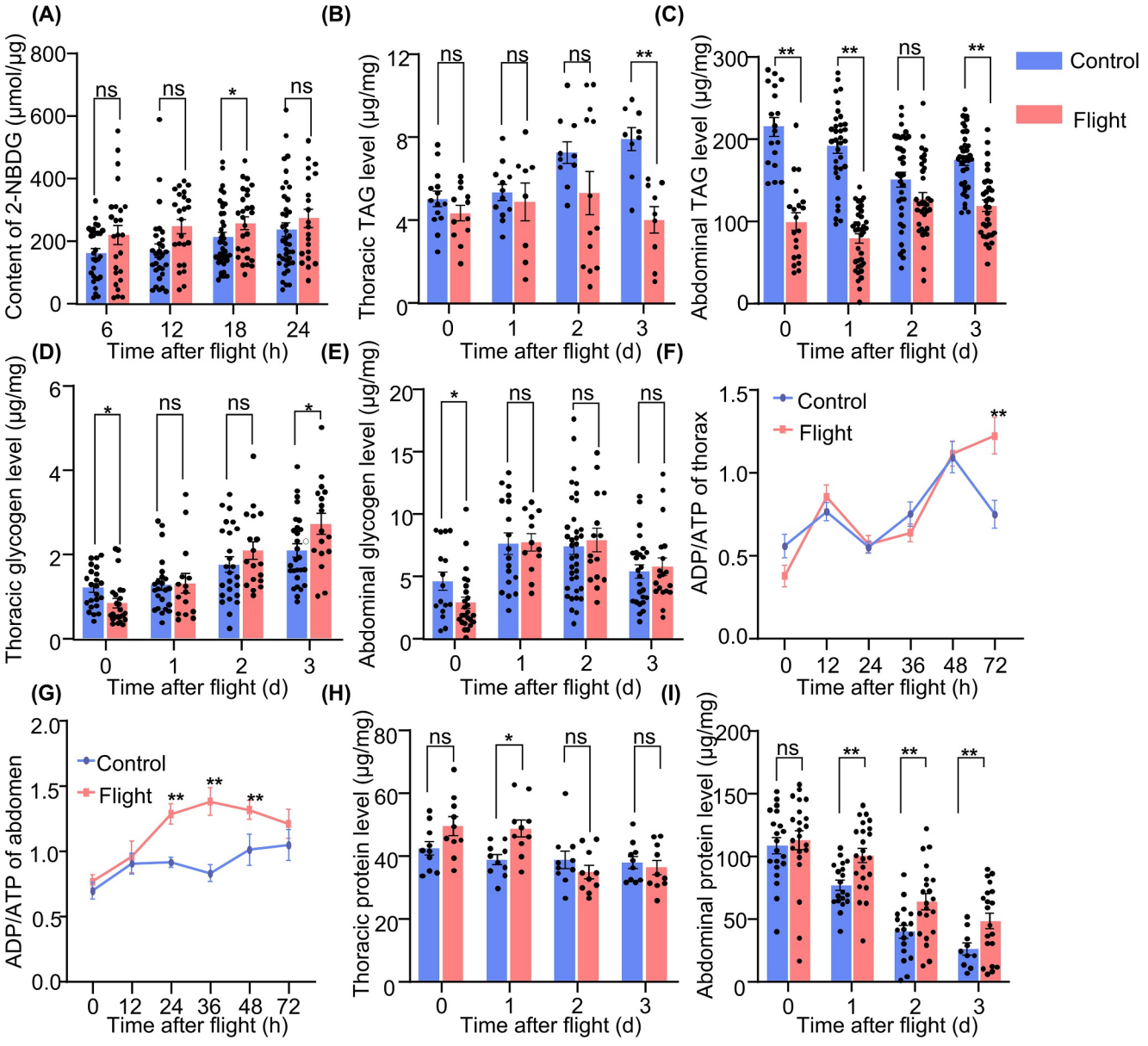

FIGURE 1 Post-flight metabolic dynamics and energy allocation in adult *Loxostege sticticalis*. (A) Feeding consumption within one day post-flight. Triglyceride content in thoracic (B) and abdominal (C) tissues during post-flight days 0–3. Glycogen content in thoracic (D) and abdominal (E) tissues during post-flight days 0–3. ADP/ATP ratio in thoracic (F) and abdominal (G) tissues during post-flight days 0–3. Protein content in thoracic (H) and abdominal (I) tissues during post-flight days 0–3. In all panels, "Flight" denotes 3-day-old females subjected to sustained flight treatment, while "Control" represents age-matched non-flight females. Post-flight sampling times (0–3 days) are indicated. Each data point represents an independent biological replicate. This convention applies to all subsequent figures. Data were analyzed by Student's *t*-test with significance levels: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$, ns, not significant.

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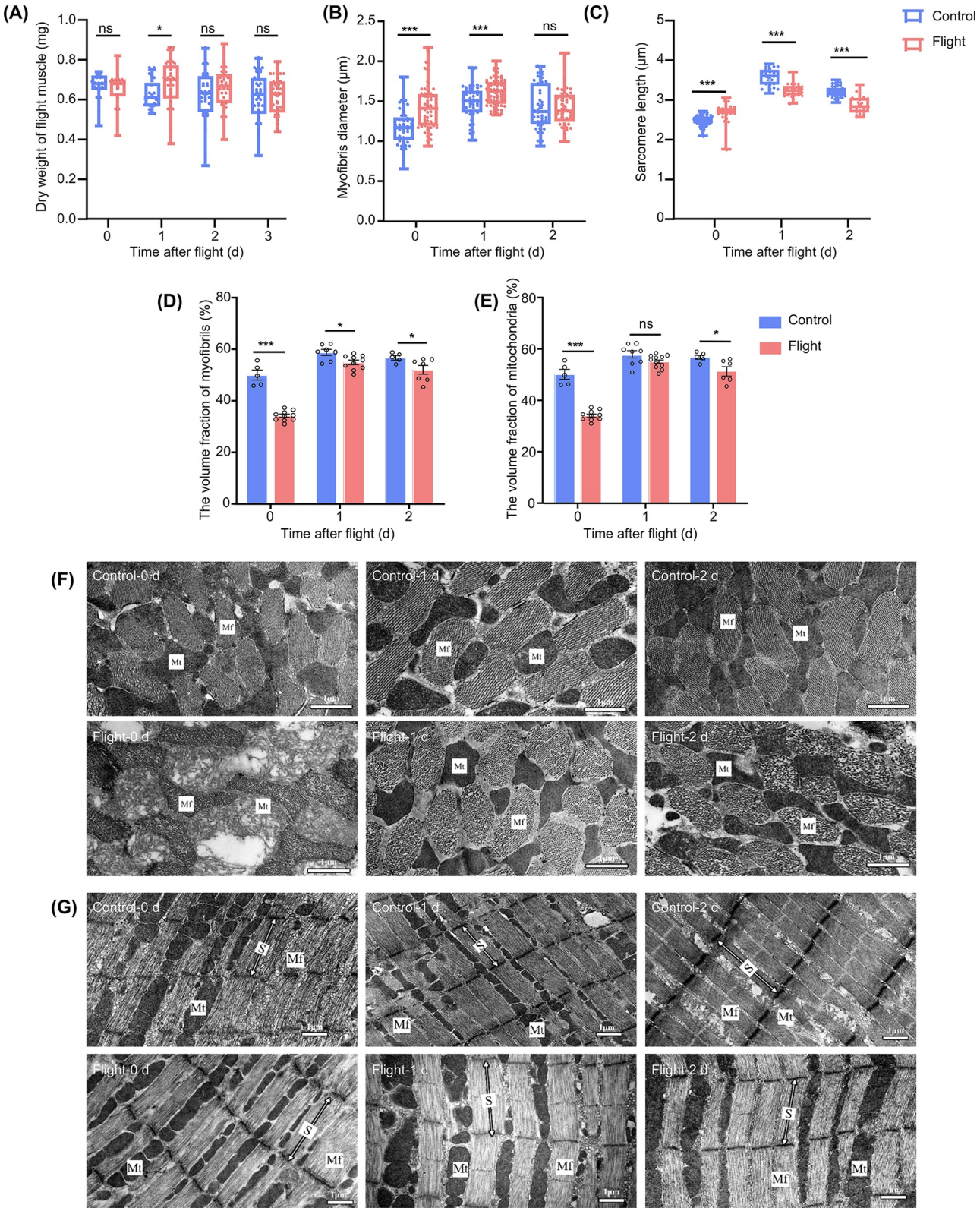

FIGURE 2 Effects of flight on dry mass and ultrastructure of flight muscles in adult *Loxostege sticticalis*. (A) The dry weight of flight muscle from 0 to 3 days post-flight. (B–E) Morphometric and volumetric parameters of flight muscles from 0 to 2 days post-flight, including myofibril diameter (B), sarcomere length (C), myofibril volume fraction (D), and mitochondrial volume fraction (E). Transmission electron micrographs of flight muscles, showing cross section (F) and longitudinal section (G). Scale bar: 1 μm (15,000× magnification). Data were analyzed by Student's *t*-test, with statistical significance levels: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Mf, myofibrils; Mt, mitochondria; ns, not significant; S, sarcomere length.

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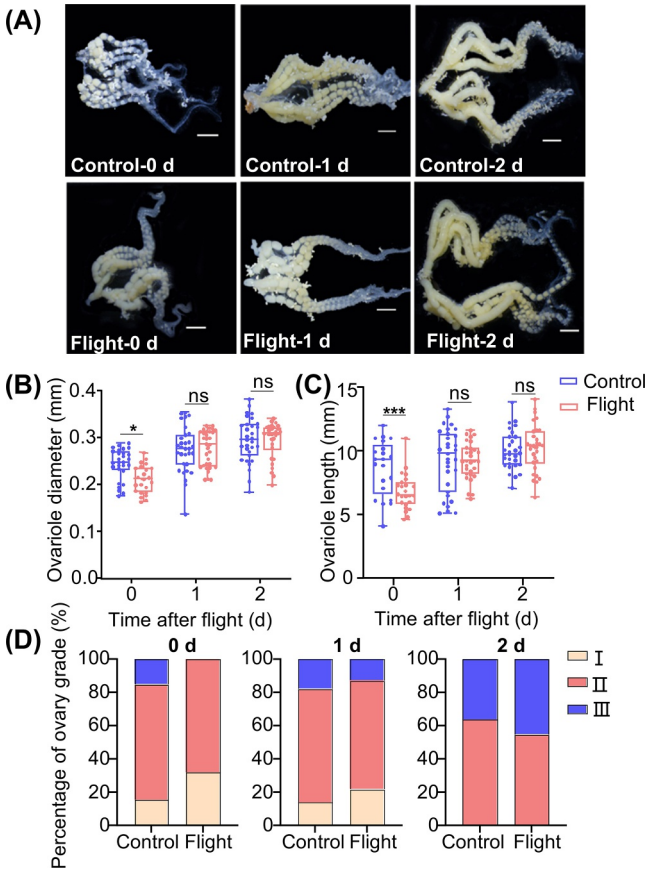

FIGURE 3 Effects of flight on ovarian development in adult *Loxostege sticticalis*. (A) Ovarian morphology from 0 to 2 days post-flight. Scale bar: 1 mm. Ovariole diameter (B) and ovariole length (C) in adults from 0 to 2 days post-flight. (D) Distribution of ovarian developmental stages from 0 to 2 days post-flight. Data were analyzed by Student's *t*-tests, with significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, ns, not significant.

3.4 | *Met* RNAi impairs flight-induced acceleration of ovarian development

As a key receptor in the JH signaling pathway, Met plays a central regulatory role in migration and reproductive development across numerous insect species. Concurrently, flight elevates JH titers and induces significant upregulation of *Met* expression in the ovaries of *L. sticticalis*, prompting the selection of *Met* for RNA interference to validate its function in flight-modulated reproduction. We analyzed ovarian development following *Met* interference (via si-*Met*) and compared the outcomes between flight and non-flight groups. Adults injected with si-*Met* at one day post-eclosion achieved peak RNAi efficiency (52.2%) at 48 h post-injection ($F_{2,6} = 31.750$, $p = 0.005$; Supporting Information S1: Figure S2), thus to maximize interference efficacy during the 3-day-old flight treatment. Compared to ddH_2O- and si-NC-injected controls, *Met* interference reduced *Kr-h1* and *Vg* expression at 4 days post-eclosion (3 days post si-*Met* injection) (Figure 5A,B), with sustained suppression observed at 6 days post-eclosion (5 days post si-*Met* injection) (Figure 5E,F). Moreover, ovariole diameter and length were significantly decreased in *Met*-interfered adults compared to controls at 4 and 6 days post-eclosion (Figure 5C,D,G,H). Furthermore, *Met* interference reduced the proportion of Stage II ovaries at 4 days post-eclosion (Figure 5I) and the proportion of Stage III ovaries at 6 days post-eclosion (Figure 5J), with delayed ovarian development observed at both time points (Supporting Information S1: Figure S3A,B). These results indicate that *Met* plays a critical role in JH-mediated reproductive regulation in *L. sticticalis*, as *Met* interference significantly reduces ovarian *Vg* expression and delays ovarian maturation. Additional reproductive parameters were also measured, revealing similar trends in the pre-oviposition period and fecundity. *Met* interference significantly prolonged the pre-oviposition period (Figure 5K) and reduced fecundity (Figure 5L).

Compared to controls with interference alone, the treatment combining interference + flight significantly decreased *Vg* expression in all groups, as well as *Kr-h1* expression in the *si-NC*/*si-NC* + *Flight* and *si-Met*/*si-Met* + *Flight* groups immediately post flight (at 4 days post-eclosion) (Figure 5A,B). Meanwhile, the diameter and length of ovarioles, along with the proportion of Stage II ovaries, were lower after flight, although no significant differences were observed except for the diameter of the *si-Met*/*si-Met* + *Flight* group (Figure 5C,D,I). Whereas, at 2 days post flight (6 days post-eclosion), the relative expression of *Kr-h1* and *Vg*, as well as ovarian development in the flight groups, were rapidly recovered or even enhanced to varying degrees compared with the levels observed immediately after flight completion (Figure 5E–H). In the ddH_2O/ddH_2O + *Flight* and *si-NC*/*si-NC* + *Flight* groups in the presence of *Met*, *Kr-h1* and *Vg* expression were induced after 2 days, bridging the differences in ovariole diameter or length while the proportions of Stage III ovaries were increased post flight (Figure 5J). These results are consistent with previous findings that flight can activate the Met/Kr-h1 pathway and promote ovarian development. However, under the conditions of *Met* gene silencing, flight can also compensate for the significantly reduced *Kr-h1* and *Vg* expression, as well as the decrease in ovariole diameter and the proportion of Stage III ovaries, but these levels always remain below those of *si-Met* non-flight groups. These findings demonstrate that *Met* is essential for flight-induced accelerated ovarian development in *L. sticticalis*. *Met* interference reduces *Met* expression and retards ovarian development, and subsequent flight treatment—normally reproductive-promoting—can only partially restore ovarian development but fails to reverse this developmental delay.

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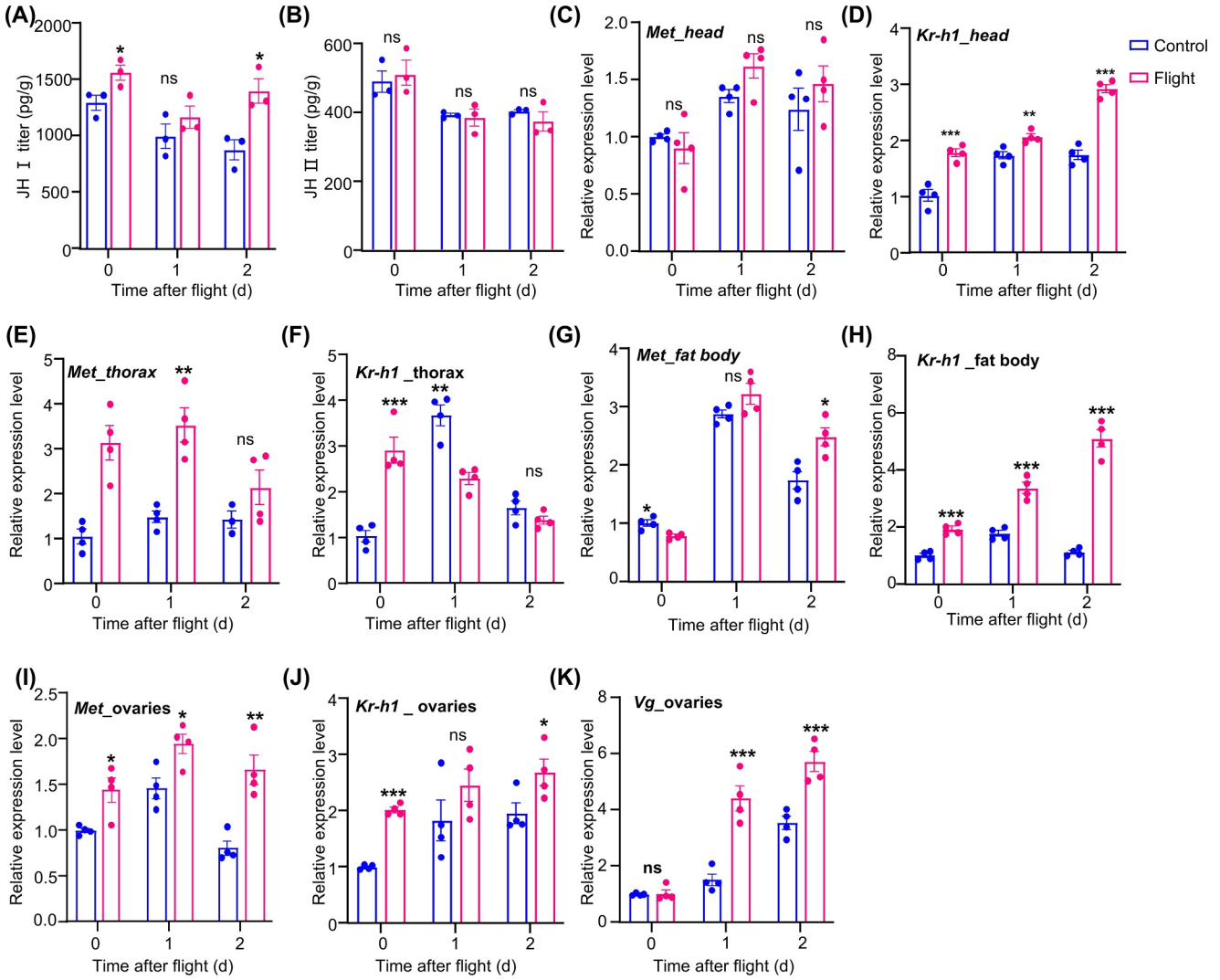

FIGURE 4 Flight-induced modulation of JH titers and the relative expression of JH-signaling genes and *Vg* in adult *Loxostege sticticalis*. (A) JH I and (B) JH II titers at 0–2 days post flight. Relative expression levels of *Met* and *Kr-h1* in heads (C–D), thoraxes (E–F), fat bodies (G–H), and ovaries (I–J) at 0–2 days post flight. (K) *Vitellogenin* (*Vg*) expression in ovaries at 0–2 days post flight. Data were analyzed by Student's *t*-test, with significance levels: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. JH, juvenile hormone; ns, not significant.

4 | DISCUSSION

Migratory insects face a significant trade-off in energy allocation between flight and reproduction.[29,44] In *L. sticticalis*, post-flight individuals resolve this conflict by increasing food intake, as evidenced by enhanced 2-NBDG accumulation (Figure 1A), accelerated vitellogenesis, and ovarian development (Figure 3A). This phenomenon is corroborated in *C. medinalis*, where insufficient energy reserves after flight lead to reduced fecundity.[45,46]

Immediately after flight cessation, *L. sticticalis* exhibits enlarged myofibril diameter and prolonged sarcomeres in flight muscles (Figure 2B,C). However, ultrastructural analysis subsequently revealed myofibril breakage (Figure 2F,G), accompanied by a reduction in thoracic protein content (Figure 1H) and decreased mitochondrial volume, alongside lowered ADP/ATP ratios in flight muscles (Figure 1F), indicating impaired oxidative phosphorylation. These findings suggest that the initial flight muscle hypertrophy represents a short-term adaptive response to flight activity, while rapid post-flight muscle histolysis likely facilitates energy reallocation to reproductive processes. This aligns with observations in crickets, where flight muscle protein depletion coincides with the initiation of ovarian development.[19] Studies on *Gryllus firmus* further demonstrate that flight muscle histolysis in long-winged morphs triggers rapid oogenesis alongside declined mitochondrial oxidative phosphorylation capacity.[20] Similarly, knockdown of myofilament protein genes in *Periplaneta americana* leads to oviposition failure in females.[47] In many migratory insects, muscle histolysis is regulated by autophagy-related genes. For instance,

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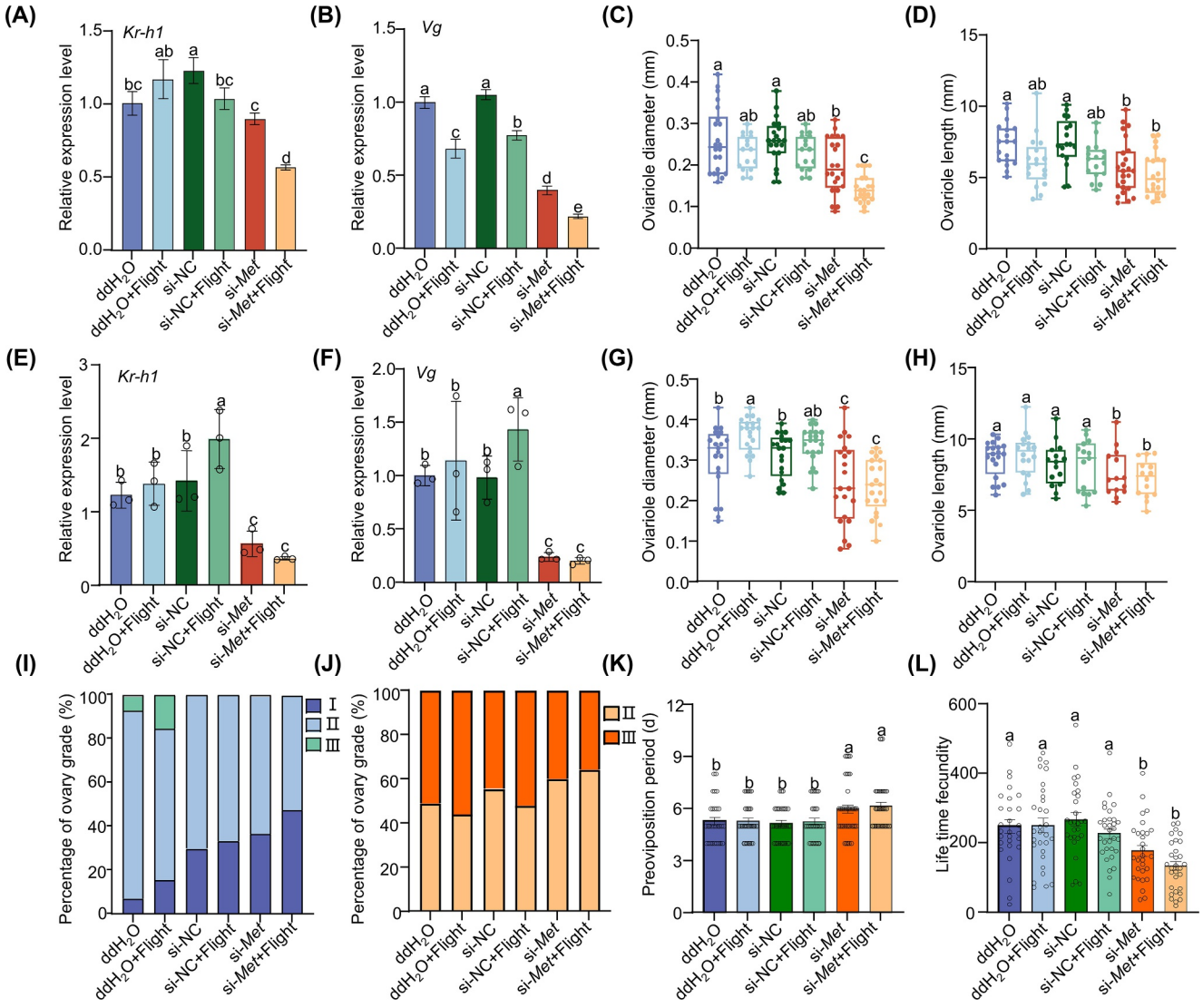

FIGURE 5 Effect of *Met* knockdown on flight-induced acceleration of ovarian development through juvenile hormone signaling in adult *Loxostege sticticalis*. (A) The relative expression of *Kr-h1* expression in ovaries measured immediately post flight (at 4 days post-eclosion). (B) The relative expression of *Vg* expression measured immediately post flight. (C) Ovariole diameter in the adults measured immediately post flight. (D) Ovariole length in the adults measured immediately post flight. (E) The relative expression of *Kr-h1* in ovaries measured 2 days post flight (at 6 days post-eclosion). (F) The relative expression of *Vg* expression in ovaries measured 2 days post flight (at 6 days post-eclosion). (G) Ovariole diameter in the adults measured 2 days post flight (at 6 days post-eclosion). (H) Ovariole length in the adults measured 2 days post flight (at 6 days post-eclosion). (I) Ovarian developmental stages measured immediately post flight. (J) Ovarian developmental stages measured 2 days post flight. (K) Pre-oviposition period. (L) Lifetime fecundity. Different lowercase letters indicate significant differences ($p < 0.05$; one-way ANOVA, Tukey's test).

in female *Laodelphax striatellus*, Beclin-mediated autophagy—a conserved lysosome-dependent histolysis process—orchestrates the physiological shift from flight muscle breakdown to reproductive acceleration via dorsal longitudinal muscle histolysis, potentially under JH regulation.[48]

Post-flight *L. sticticalis* adults show dynamic TAG fluctuations, with a rapid recovery followed by a decline (Figure 1B,C), synchronizing with ovarian maturation. Given that low TAG levels impair reproduction in *M. separata*,[49,50] the rapid TAG recovery within 48 h post flight likely supports subsequent reproductive investment in *L. sticticalis*. The subsequent TAG reduction mirrors observations in *C. medinalis*, where a decline in TAG levels by day 3 post-flight coincides with accelerated ovarian development.[51] Concurrently, thoracic glycogen displays initial depletion followed by a compensatory overshoot above control levels by day 3 (Figure 1D), collectively indicating the progressive recovery of energy reserves and their reallocation to reproduction to facilitate early oviposition.[8]

Flight-induced compensatory feeding and muscle histolysis redirect energy toward ovaries, alleviating transient post-flight ovarian suppression while

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promoting development (Figure 3B). This life-history-driven resource allocation is mediated by the upregulation of hemolymph amino acid transporters, which activate the TOR pathway to drive TOR-dependent *Vg* expression and increase abdominal protein content (Figure 1I).[52] Additionally, flight-stimulated JH directly initiates *Vg*-mediated vitellogenesis via the *Met*/Kr-h1 axis (Figure 4B). RNAi-mediated *Met* knockdown in *L. sticticalis* decelerated ovarian development, prolonged pre-oviposition periods, reduced egg production, and rendered flight-induced reproductive promotion irreversible (Figure 5), confirming JH's pivotal role in resolving the dispersal-reproduction conflict through coordinated energy reallocation within limited life-history periods.[53] Previous studies indicate that newly established populations require only 50% of the emigrant population density to trigger outbreak-scale growth in the next generation.[35] These advances deepen our mechanistic understanding of flight-driven outbreaks in *L. sticticalis* while clarifying the flight-outbreak nexus. Nevertheless, flight-enhanced reproduction involves multidimensional regulatory mechanisms beyond JH signaling, warranting further investigation into endocrine crosstalk (e.g., ecdysteroids and insulin-like peptides) in post-flight reproductive optimization.

5 | CONCLUSION

This study reveals that flight activity in sexually immature female *L. sticticalis* adults activates a dual regulatory mechanism to resolve the energetic trade-off between migration and reproduction. Flight induces two interconnected processes: nutrient acquisition through increased feeding and flight muscle histolysis marked by myofibrillar disassembly and mitochondrial degeneration. These mechanisms collectively redirect energy substrates—including TAGs, glycogen, and amino acids—to fuel ovarian maturation. Simultaneously, flight stimulates JH biosynthesis, which activates the JH receptor *Met* and its downstream effector *Kr-h1*, thereby enhancing vitellogenin transcription and yolk deposition. Crucially, RNAi-mediated suppression of *Met* abolished flight-triggered reproductive advantages, demonstrating the indispensable role of the JH-*Met*/*Kr-h1* pathway in linking flight-derived energy reallocation to ovarian development. These adaptive processes synchronize oviposition timing and augment fecundity by repurposing nutrients from degraded flight muscles and optimizing post-migratory energy allocation. By unraveling the endocrine-metabolic interplay governing flight-reproduction coordination, this work advances our understanding of adaptive strategies in migratory pests and identifies JH signaling as a potential target for disrupting life-history synchronization, thereby offering a novel molecular perspective for mitigating population outbreaks of this ecologically significant species.

AUTHOR CONTRIBUTIONS

Yu Gao: Writing—original draft; investigation; visualization; data curation; writing—review and editing. **Yunxia Cheng**: Conceptualization; data curation; writing—review and editing. **Wenyi Song**: Investigation; visualization; writing—review and editing. **Lei Zhang**: Software; resources. **Dianjie Xie**: Software; project administration; writing—review and editing. **Xingfu Jiang**: Funding acquisition; writing—review and editing; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

Ethical approval and permits were not required as no protected or endangered species were involved, and all specimens were collected/handled in compliance with local regulations on non-vertebrate organisms.

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