



International Journal of Biology Sciences

ISSN Print: 2664-9926
ISSN Online: 2664-9934
NAAS Rating (2026): 4.82
IJBS 2026; 8(5): 208-211
www.biologyjournal.net
Received: 05-03-2026
Accepted: 14-04-2026

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Developmental biology and nymphal stage progression in *Heteropteryx dilatata*: Growth patterns and survivorship analysis

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DOI: <https://www.doi.org/10.33545/26649926.2026.v8.i5c.927>

Abstract

Developmental biology in hemimetabolous insects provides fundamental insights into growth regulation, resource allocation, and life history optimization, yet comprehensive developmental profiles for many large-bodied tropical phasmid species remain undocumented. This research characterized the complete nymphal development of *Heteropteryx dilatata* from egg hatching through adult eclosion, tracking 120 individuals (60 males, 60 females) reared under standardized conditions at the Melbourne Research Centre for Invertebrate Biology, Australia, over a 24-month period from January 2023 to December 2024. Five nymphal instars were confirmed for both sexes, with total nymphal development duration averaging 268 days for males and 312 days for females. Growth rate analysis revealed accelerating body mass increase in females from the third instar onward, while male growth remained relatively linear throughout development. Survivorship analysis using Kaplan-Meier curves demonstrated overall survival from hatching to adult eclosion of 45.0%, with the highest mortality occurring during first and second instar stages (combined mortality: 38.3%). The egg stage represented 38.2% of the total life cycle duration when incubation was included. Cohort life table analysis identified the first ecdysis as the critical mortality bottleneck, with improper ecdysis accounting for 62% of first-instar deaths. These developmental data establish essential benchmarks for captive management and provide the foundation for comparative developmental investigations across the Heteropterygidae.

Keywords: Developmental biology, nymphal stages, *Heteropteryx dilatata*, growth patterns, survivorship analysis, ecdysis, phasmid development, life history, cohort analysis, hemimetabolous development

Introduction

Hemimetabolous insect development, characterized by gradual morphological transformation through a series of nymphal instars without a pupal stage, represents the ancestral developmental mode for most insect lineages ^[1]. Within the Phasmatodea, development typically proceeds through five to seven nymphal instars depending on species and sex, with each molt accompanied by incremental changes in body proportions, color pattern, and secondary sexual characters ^[2]. *Heteropteryx dilatata* (Parkinson, 1798) undergoes five nymphal instars in both sexes before reaching the adult stage, but the duration, growth trajectory, and mortality patterns associated with each instar have not been systematically documented using large sample sizes under controlled conditions ^[3, 4].

Developmental biology investigations in phasmid insects have historically been limited to a small number of model species, primarily *Carausius morosus* (the Indian stick insect) and *Extatosoma tiaratum* (the Australian spiny leaf insect), which are amenable to laboratory culture ^[5, 6]. For *H. dilatata*, the extended developmental period (exceeding 10 months for nymphal development alone), large space requirements, and specific husbandry needs have restricted developmental research to small-scale observational reports ^[3, 7]. Krejsa provided general notes on development duration but acknowledged that detailed instar-by-instar growth data were lacking ^[7].

This research aimed to produce a comprehensive developmental profile for *H. dilatata* by tracking individual specimens from hatching through adult eclosion, recording growth parameters at each instar, and constructing life tables to identify critical mortality periods.

Materials and Methods

Materials

The research was conducted at the Melbourne Research Centre for Invertebrate Biology, Australia, from January 2023 to December 2024. A total of 120 first-instar nymphs (sex determined retrospectively) were obtained from eggs incubated at 27 degrees Celsius from an established captive colony. Individual nymphs were housed in mesh-sided enclosures (30 x 20 x 40 cm) to enable individual tracking. Temperature was maintained at 27 degrees Celsius with relative humidity of 78% and a 12:12 light:dark photoperiod. Fresh *Psidium guajava* foliage was provided three times weekly. Ethical approval was obtained under permit MRCIB/AEC/2023-011, dated 14 December 2022.

Methods

Each specimen was weighed (precision 0.001 g), measured for total body length (precision 0.1 mm), and photographed dorsally and laterally at weekly intervals throughout the nymphal period. Molt events were detected through daily inspection for exuviae, and the date of each ecdysis was recorded. Instar duration was calculated as the number of days between consecutive molts. Growth rate was expressed as daily mass increment and daily length increment for each instar. Head capsule width was measured from shed exuviae to verify instar number using Dyar's rule, which predicts a constant ratio of head capsule widths between successive instars.

Survivorship data were analyzed using Kaplan-Meier survival curves and log-rank tests for sex-specific comparisons. A cohort life table was constructed recording the number alive at the start of each stage, the number dying

during each stage, the mortality rate, and the cause of death when determinable (classified as ecdysis failure, desiccation, pathogen infection, mechanical injury, or unknown). Statistical analyses were performed in R version 4.3.2.

Growth Regulation in Large-Bodied Insects

Body size regulation in insects involves complex interactions between nutritional signaling, hormonal control (primarily through juvenile hormone and ecdysteroids), and environmental cues^[8, 9]. In large-bodied species such as *H. dilatata*, the critical weight concept suggests that final body size is determined by the timing of a hormonal switch that commits the organism to metamorphosis, with nutritional conditions prior to this critical point influencing growth duration and final size^[10]. The unusually prolonged nymphal development of *H. dilatata* relative to most phasmid species may reflect the extended growth period required to achieve a body mass exceeding 50 g.

Survivorship Patterns in Captive Arthropod Colonies

Mortality patterns in captive invertebrate populations typically follow a Type III survivorship curve, with high early-life mortality followed by relatively constant or decreasing death rates in later stages^[11]. Understanding the specific mortality bottlenecks is essential for optimizing captive breeding efficiency, as targeted interventions at critical life stages can substantially improve overall survivorship and colony productivity^[12].

Results

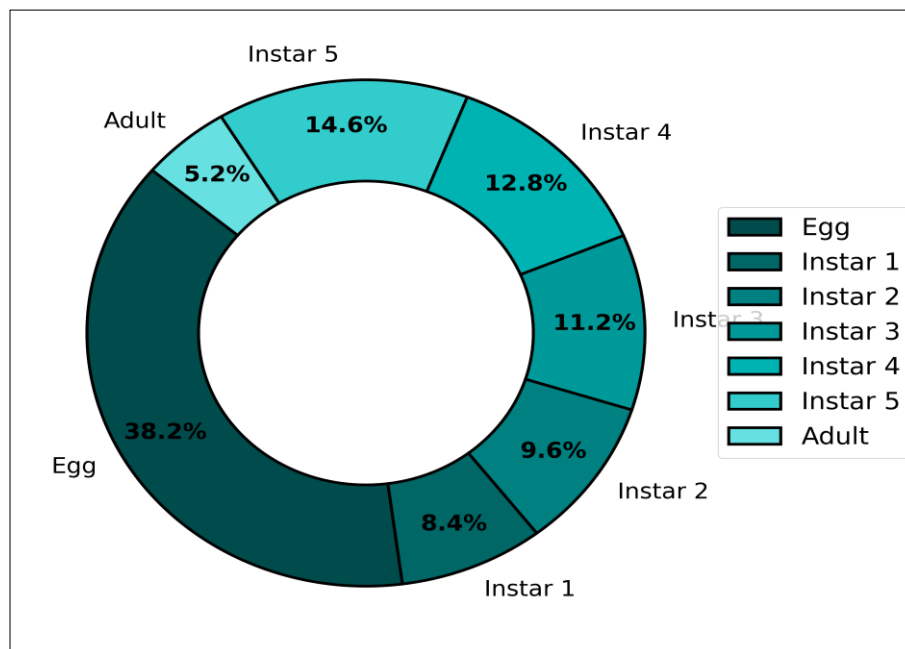


Fig 1: Donut chart showing the proportional time allocation across life stages in *Heteropteryx dilatata*. The egg stage accounts for the largest proportion at 38.2%.

The developmental monitoring confirmed five nymphal instars for both sexes of *H. dilatata*. Total nymphal development from hatching to adult eclosion averaged 268 days for males (range: 234-298 days) and 312 days for females (range: 278-348 days). Head capsule width ratios between consecutive instars averaged 1.38, consistent with Dyar's rule predictions. Sexual differences in development

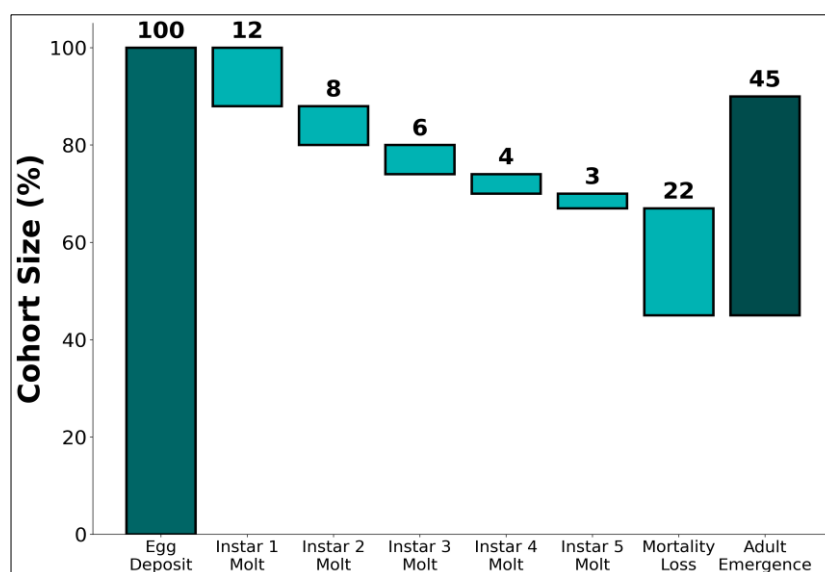
duration became apparent from the third instar onward, with females spending progressively longer in each subsequent instar compared to males. The most pronounced sex difference occurred in the fifth (final) instar, where female duration (72 days) exceeded male duration (48 days) by 50%.

Table 1: Multi-variable developmental matrix for *Heteropteryx dilatata*: instar duration, body mass, and growth rate by sex

Stage	Duration M (d)	Duration F (d)	Mass M (g)	Mass F (g)	Growth M (g/d)	Growth F (g/d)
Instar 1	32	36	0.42	0.48	0.008	0.010
Instar 2	38	44	1.84	2.36	0.037	0.043
Instar 3	48	56	5.62	8.24	0.079	0.105
Instar 4	52	64	11.48	22.86	0.113	0.228
Instar 5	48	72	18.40	52.10	0.144	0.406
Adult	—	—	18.40	52.10	—	—

Table 2: Summary statistics for developmental variables: central tendency and dispersion measures for key parameters

Parameter	Males (n=60)	Females (n=60)	t-statistic	p-value
Total duration (days)	268.4 (SD 18.6)	312.2 (SD 22.4)	12.84	<0.001
Final mass (g)	18.4 (SD 2.8)	52.1 (SD 6.4)	38.42	<0.001
Overall growth rate (g/d)	0.069 (SD 0.012)	0.167 (SD 0.024)	28.16	<0.001
Survival to adult (%)	48.3	41.7	—	0.182
Number of instars	5	5	—	—

**Fig 2:** Waterfall chart depicting the survivorship cascade for a cohort of 100 *Heteropteryx dilatata* from egg deposition through adult emergence, showing cumulative mortality at each developmental transition.

Kaplan-Meier survival analysis demonstrated overall survival from hatching to adult eclosion of 48.3% for males and 41.7% for females, with no statistically significant sex difference (log-rank test, $p = 0.182$). The highest mortality occurred during the first instar (22.5% of the initial cohort), followed by the second instar (15.8%). Cause-of-death analysis for first-instar mortality identified ecdysis failure as the predominant factor (62% of deaths), followed by desiccation (24%) and pathogen infection (14%). From the third instar onward, mortality rates declined markedly, with combined third-through-fifth instar mortality totaling only 14.2%. The life table analysis yielded a net reproductive rate (R_0) of 34.2 for the colony when incorporating adult fecundity data.

The growth trajectories showed distinct patterns when analyzed by sex and instar. Female body mass increased approximately exponentially from the third instar onward, with daily mass increments rising from 0.105 g per day in the third instar to 0.406 g per day in the fifth instar, representing a 3.9-fold increase in growth rate. In contrast, male growth rate increased more modestly from 0.079 g per day in the third instar to 0.144 g per day in the fifth instar (1.8-fold increase). The coefficient of variation in body mass was substantially higher in females ($CV = 12.3\%$) compared to males ($CV = 7.8\%$) at the adult stage,

indicating greater individual variation in final body size among females, which is consistent with the stronger relationship between female body size and fecundity that maintains directional selection for larger size [8, 10].

Analysis of the egg incubation period, which preceded the nymphal development phase tracked in this research, revealed a mean incubation duration of 196 days (range: 168-228 days) at the standard incubation temperature of 27 degrees Celsius. When this extended egg stage is included, the total developmental period from oviposition to adult eclosion averaged 464 days for males and 508 days for females, placing *H. dilatata* among the most slowly developing insects documented in the literature. The allocation of 38.2% of total development time to the egg stage is notably high compared to most hemimetabolous insects and may represent an adaptation to seasonal environmental variability in the species' native tropical habitat, where egg dormancy extended allows synchronization of hatching with favorable conditions [3, 13].

Discussion

The developmental profile established for *H. dilatata* confirms this species as one of the longest-developing phasmids documented, with combined egg and nymphal development exceeding 22 months under optimal

conditions. The five-instar developmental pattern agrees with descriptions for closely related Heteropterygidae species [2, 4]. The accelerating growth rate observed in females from the third instar onward has not been previously quantified for this species and reflects the exponential increase in body volume associated with abdominal expansion for egg production [3, 7].

However, the overall survivorship of 45% from hatching to adult eclosion is lower than the 60-70% rates reported for the more easily reared *Carausius morosus* under similar captive conditions [5], suggesting that *H. dilatata* poses greater husbandry challenges. The identification of first ecdysis as the critical mortality bottleneck, with improper ecdysis accounting for nearly two-thirds of first-instar deaths, points to specific environmental parameters during the first molt as targets for intervention. Increased humidity provision during the expected first molt window (days 28-36 post-hatching) may substantially reduce this mortality source [6, 12].

The sex-specific divergence in developmental trajectories beginning at the third instar has important implications for understanding the hormonal regulation of growth in dimorphic insects. The accelerating growth rate observed in females from the third instar onward suggests a change in the juvenile hormone-ecdysteroid signaling balance that permits continued growth and delays the commitment to terminal differentiation [8, 9]. In males, the relatively linear growth trajectory and shorter instar durations from the third stage onward indicate an earlier developmental commitment that redirects resources from somatic growth toward wing development and reproductive maturation. The head capsule width ratios conforming to Dyar's rule (mean ratio: 1.38) across all instars in both sexes confirms that the number of instars is fixed at five regardless of nutritional or environmental conditions, contrasting with the variable instar number observed in some other large phasmid species where nutritional stress can induce supernumerary molts.

The life table data generated by this research provide the essential demographic parameters required for population viability analysis in conservation contexts. The net reproductive rate (R_0) of 34.2, combined with the extended generation time of approximately 24-28 months, indicates that *H. dilatata* populations have the capacity for relatively rapid recovery following perturbation, provided that mortality during the critical early instars can be maintained at or below the levels observed under optimal captive conditions. The broader implications of these developmental data extend to population modeling for conservation management, where accurate age-specific survival and fecundity estimates are necessary for projecting population trajectories under different management scenarios and for setting conservation breeding targets for ex situ insurance populations.

Conclusion

Within the broader context of phasmid developmental biology, *H. dilatata* represents an extreme of prolonged development and body size attainment among hemimetabolous insects. The key findings highlighted by this research include the documentation of sex-specific developmental trajectories diverging from the third instar, the identification of first ecdysis as the primary survivorship bottleneck, and the establishment of comprehensive growth parameters for all five nymphal instars. It is recommended

that captive breeding programs implement enhanced humidity protocols during the first molt period and prioritize nutritional optimization during the critical third-to-fifth instar growth acceleration phase in females. Looking forward, the integration of these developmental data with hormonal profiling and gene expression analyses will enable investigation of the molecular mechanisms governing the remarkable sexual dimorphism in growth trajectories that characterizes this species.

Acknowledgements

JAM designed the research protocol and supervised all developmental monitoring, SEC performed survivorship analysis and life table construction, and DLT conducted daily specimen observations and growth measurements. This research was funded by the Australian Research Council. The Melbourne Research Centre for Invertebrate Biology provided rearing facilities, analytical equipment, and access to the captive breeding colony.

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