Canopy parkour: movement ecology of post-hatch dispersal in a gliding nymphal stick insect (*Extatosoma tiaratum*)

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Abstract

For flightless arboreal arthropods, to move from understory toward tree canopies is cognitively and energetically expensive, because various vegetational structures form complex three-dimensional landscapes with air gaps. The exposure to predation and environmental perturbations in the canopy space further obstruct the movement process. How to effectively move through the canopy space thus requires effective navigation tactics and movement skills. In the Australian stick insect *Extatosoma tiaratum*, the first instar nymphs hatch on the forest floor and disperse toward tree canopies in the daytime. Here, we address the movement ecology of dispersal in the *E. tiaratum* nymphs under controlled laboratory conditions. We found the newly hatched nymphs ascend with high endurance, accomplishing 100+ m within 60 minutes. Their navigation toward open canopies is generally directed by negative gravitaxis, positive phototaxis and tactic response to vertically oriented contrast patterns. We also found nymphal *E. tiaratum* use directed jumping to cross air gaps and respond to tactile stimulations and potential threat with self-dropping reflexes, actions which both lead to aerial descent. In sum, the post-hatch dispersal in *E. tiaratum* consists of various visually mediated movements both on vegetational structures and in air, within which context gliding is an effective mechanism for height recovery after predator- and perturbation-induced descent. These results further support the fundamental role of a diurnal temporal niche, in addition to spatial niche, to the evolution of gliding in wingless arboreal invertebrates.

Keywords

canopy, gliding, invertebrate, intermittent locomotion, jumping, ontogeny, tactic behavior

Symbols and abbreviations

GLMM	generalized linear mixed model
θ	circular direction of von Mises distribution
κ	concentration parameter of von Mises distribution

1. Introduction

Flightless nymphal and adult arthropods compose the majority of arboreal invertebrate fauna (Basset, 2001; Basset et al., 2012), and they crawl on vegetational structures (e.g., tree trunks and liana) for various life activities (e.g., locating resources, dispersal and homing after dislocation) (Cunha and Vieira, 2002; Basset et al., 2003; Yoshida and Hijii, 2005). Nevertheless, legged movements by small invertebrates are potentially challenged by the three-dimensional landscape and dynamic environment in the canopy space. First, for small invertebrates in legged movement, the rough terrains formed by different vegetational structures (e.g., foliage, branches, and stems) preclude straight movement paths and may obstruct directed movements with air gaps. In particular, vertical movements between forest floor and canopies cover relatively long distances (e.g., forest canopy height ranges 8 – 40 m globally; Simard et al., 2011). Second, the complexity and dynamics of physical environment challenge the navigational process and movement performance. Diverse vegetational structures form highly heterogeneous visual environments under sunlight, with sunflecks and shadows projected onto various surfaces. The visual environment thus changes with time and the observer's perspective, challenging the use of long-range visual cues. Also, as invertebrates' movement endurance is by the environmental temperature (Full and Tullis, 1990), the daily cycle of temperature in forests (e.g., ~10˚C day-night difference; Shuttleworth, 1985) may constrain the time and height of movement activities. Third, exposure to predators and parasitoids, many of which are specialized for searching or ambushing prey or host on vegetational surfaces (e.g., insects, spiders and birds; Southwood et al., 1982; Russell-Smith and Stork, 1994; Ford et al., 1986; Basset, 2001), also risk small invertebrates' movements through the canopy space. In addition to biological threats, climatic perturbation (e.g., rain and wind gusts; McCay, 2003) can also interfere with directed movements. Therefore, arboreal transport by small invertebrates is cognitively and energetically costly, requiring cognitive and locomotor capabilities for navigating through the complex space. Such demand may be particularly strong for vertical transport given the vertical variation of microhabitats and ecosystems (Erwin, 1988; Shuttleworth, 1985).

Despite the spatiotemporal variation of visual environment, gravity and sunlight may serve as basic long-range cues in canopy space. Land arthropods generally perceive gravity with gravireceptors and integrate it with other signals (e.g., visual) for navigation (Büschges et al., 2001; Brockmann and Robinson, 2007; Robie et al., 2010). Also, a light gradient in space may be used to refer the direction of sun and foliage coverage (Bjorkman and Ludlow, 1972; Endler, 1993; Wolken, 1995), with the strongest signal strength and lowest temporal variation during the midday (i.e., a peak plateau of solar altitude with < 5˚ variation between 11am and 1pm). In addition, vegetational structures under sunlight likely provide short-range visual cues for spatial discrimination. For example, insects identify contrast edges for landing (Kern et al., 1997; Zeng et al., 2015). The uses of gravitational and visual cues are potentially more general than chemical cues, which generally depends on a strong source (e.g., airborne odor from flowers) or consistency (e.g., pheromone trails used by ants; Jackson et al., 2007).

Arboreal invertebrates have many adaptations for movement within canopy space. Jumping is a common strategy for crossing air gaps (Graham and Socha, 2019), providing an energetically more efficient mechanism than detouring. Besides missed landings after jumping, other types of accidental losses of foothold (e.g., perturbation by weather or larger animals) and defensive self-dropping (e.g., startle response; Haemig, 1997; Humphreys and Ruxton, 2019; Dudley and Yanoviak, 2011) can lead to aerial descent. Free fall initiation is fundamental to the evolution of directed aerial descent (noted as 'gliding' hereafter), which reduces the height loss after descent (Dudley and Yanoviak, 2011; Zeng et al.,

2016). However, an arboreal spatial niche is inadequate for the evolution of gliding, as suggested by the incapability of gliding in many tree-dwelling ants (Yanoviak et al., 2011). On the other hand, a diurnal temporal niche, which permits visually-mediated aerial maneuver and landing, may also be essential for the evolution of gliding (Yanoviak et al., 2011; Zeng et al., 2015). Studying the ecology of movement in canopy space and the mechanisms of aerial descent initiation can thus help addressing the utility of gliding within a taxa-specific ecological context.

The newly hatched nymphs of the Australian stick insect *Extatosoma tiaratum*, Macleay 1826 disperse by ascending from forest floor, where eggs are deposited, to the tree canopies (**Fig. 1A,B**). Unlike the generally conspicuous and nocturnally active lifestyle of phasmids, *E. tiaratum* nymphs hatch during midday (i.e., 11 a.m. to 3 p.m.) of rainy seasons (November to January; Carlberg, 1981, 1983, 1984; Brock and Hasenpusch, 2009; Brock, 2001) and immediately start moving hyperactively. They also exhibit ant-mimicking coloration and behaviors (e.g., body shaking during crawling; **Fig. 1**; **Movie S1**), while constantly climbing and exploring the space (Carlberg, 1981, 1983; Rentz, 1996). These traits collectively form a disperser's syndrome (Ronce and Clobert, 2012) that potentially facilitates the ascending dispersal and search for suitable microhabitats. During dispersal, they likely glide to reduce the height loss after falls (Zeng *et al.*, 2015). This post-hatch dispersal behavior is only exhibited during the first 3–5 days after hatching, during which the nymphs become nocturnally active and lose the ant-mimicry (**Fig. 1B**) (Brock, 2001; Brock, 1999).

Here, we study the movement ecology of canopy dispersal in newly hatched *E. tiaratum* under controlled laboratory conditions, focusing on their navigational and movement mechanisms for traveling through the canopy space. We hypothesize: (1) the dispersing nymphs use of gravity, light gradient and visual contrasts for navigating toward vegetational structures, which are used as corridors for ascending; (2) the newly hatched nymphs are capable of accomplish long-distance ascending; (3) when dispersing, newly hatched nymphs can initiate aerial descent through both active mechanisms (e.g., jumping) and passive mechanisms (e.g., response to tactile perturbation). Within this context, the navigation tactics and motion capacity together determine the movement process of individual dispersing insects through both vegetational structures and air gaps (**Fig. 1C**) (see 'movement ecology paradigm'; Nathan et al., 2008). Understanding this process can provide general framework for understanding movement ecology of small wingless invertebrates in canopy space and help to address the behavioral ecological context of the utility of gliding.

2. Results

2.1 Negative gravitaxis

After being released to a vertically oriented T-maze within a visually homogeneous environment (**Fig. 2A**), experimental insects moved to the intersection and ascent along the vertical rod under various environmental luminances (0 lx – 3000 lx), exhibiting frequencies of gravitaxic response (f_g) significantly different from the null (**Fig. 2B**). This result supported our hypothesis that gravity alone can be used by nymphal *E. tiaratum* as a directional cue. Furthermore, the ascending frequency was inversely correlated with the environmental luminance (coef. = -0.0013 ± 0.0002, $P < 0.0001$, Poisson GLMM) in newly hatched (0-day-old) nymphs, with the greatest frequency (f_g ~1) under total darkness (**Fig. 2B**).

2.2 Positive phototaxis

After being released into a T-maze made of dark tunnels, experimental insects moved into an experimentally controlled luminance gradient, where the mean luminance ranged between ~2 lx and 1.5×10^4 lx (**Fig. 3A**). Newly hatched nymphs (0-day-old) exhibited strong phototaxic movements under all conditions, with the frequency of phototaxic response $f_p > 0.8$ under all light conditions. Overall, f_p declined with both age and increasing mean luminance (**Fig. 3B**). For example, 10-day-old nymphs tended to move toward the darker direction when the mean luminance exceeded 1.5×10^4 lx. In control experiments with no luminance gradient, the insects showed non-significant directional bias (repeated G-test: $G = 0.722$, d.f. = 1, $P = 0.396$). This result supported the hypothesis that nymphal *E. tiaratum* use luminance gradient alone as directional reference.

2.3 Tactic movement toward visual contrasts

Experimental insects were released into a visual arena surrounded by vertically oriented contrast lines (**Fig. 4A**; **Movie S1**). With contrast patterns formed by equally sized surfaces (black-white, black-gray, and gray-white), insects rapidly moved toward the contrast lines (**Fig. 4B**), showing the strongest directional preference to black-gray contrast (**Fig. 4C**; **Supplementary Table S1**). When exposed to black-gray contrasts, they also exhibited the fastest movement speed (~3.5 cm/s) on the arena floor and initiated climbing immediately after reaching the wall (< 2 s) (**Fig. 4D,E**). Black-white and gray-white contrasts were less attractive; the insects showed the slowest movement when exposed to gray-white contrast. Furthermore, when exposed to contrast patterns formed between surfaces of different sizes, the insects showed a general preference to the narrower surface regardless of its brightness. In such contrast patterns formed between black and white surfaces, the frequencies of moving toward narrower surface was significantly greater than the null expectation (**Fig. 4F,G**). The tactic response to vertically oriented contrast lines and preference to narrower surface may help locating vegetational structures to initiate ascending (see Discussion).

2.4 Ontogenetic decline of ascending endurance

We sampled the ascending behavior of nymphal *E. tiaratum* in six age groups between 2-hour-old and

240-hour-old. Experimental insects were placed on a vertically oriented treadmill with speed control and filmed for 60 min (**Fig. 5A**). The ascending motion on treadmill was then digitized to generate speed profiles, which consists of intermittent ascending and pausing intervals (**Fig. 5B**). Further analyses showed an ontogenetic decline of ascending capability. First, the ascending speed (ranged 2.3–5.3 cm/s) generally declined with increasing age. The 4-hour-old and 48-hour-old nymphs exhibited the greatest speed, showing a peak within the first three days after hatching (**Fig. 5C**). The low ascending speed in 2-hour-old nymphs is due to frequent pauses (**Fig. 5D**). Second, the 2-hour-old nymphs exhibited the highest ascending endurance, with the greatest ascending time (> 90% active time) and total ascent height (100+ m); the older (> 5-day-old) nymphs were only active for < 1 min and remained immobile throughout the rest of the trial (**Fig. 5D**,**E**).

2.5 Predator- and perturbation-induced self-dropping

Experimental insects were tested with two tactile perturbations, simulated predatory attacks and accidental losses of foothold (see Methods). (1) In the newly hatched nymphs, simulated attacks led to self-dropping (**Fig. 6A,B**). On the contrary, older nymphs generally exhibited evasion by inclining away from the direction of attack. High-speed filming revealed that the self-dropping was initiated by voluntary withdrawal of tarsus from the substrate within ~50 ms after the removal of simulated attack, followed by a midair tucking (flexion of tibia-femur joint and elevation of femur) of all leg pairs (N = 30 trials; **Fig. 6A**; **Movie S3**). (2) When stepping on a slippery surface during ascending, the experimental insects were subjected to an unexpected sudden unbalance and loss of foothold (**Fig. 6C**). The newly hatched nymphs (0-day-old) exhibited self-dropping behavior with a frequency of 55.9 ± 6.7% (mean ± s.e.m.; **Fig. 6D**). High-speed videos revealed that, after the loss of foothold by one leg, other leg pairs showed similar flexion and tucking as described above, leading to removal of tarsi from the substrate and self-dropping (**Movie S4**). Self-dropping after touching the slippery surface was not observed in older nymphs.

2.6 Jumping for crossing air gaps

To test if nymphal *E. tiaratum* jump to cross air gaps, we introduced them to an elevated platform with a distant visual target, either a horizontal rod or a vertical rod in contrast with a white background (**Fig. 7A**). After ascending to the platform, the insects typically oriented toward the visual target, explored the space and tried to reach out using forelegs. Once failed to reach with forelegs, the youngest insects (0-day-old) would jump toward the visual target (**Fig. 7B**; **Movie S5**), as observed in 19 out of 24 tested individuals. When exposed to the horizontal target, the insect spent 1.8±0.2 min (mean ± s.e.m., N = 28 trials) before jumping and successfully landed on the target in 17 out of 28 trials (success rate ~60%); based on trials with successful landing, they traveled a horizontal distance 8.2±1.6 cm with a 20 cm descent, showing a distance ratio of horizontal to vertical ~0.41. When exposed to the vertical target, the insects spent 2.8±0.3 min (N = 21 trials) before jumping and successfully landed in 13 out of 23 trials (success rate ~56%); based on trials with successful landing, they descent 14.4±6.1 cm with an 8 cm horizontal translation, showing a distance ratio of horizontal to vertical ~0.55. On the contrary, jumping behavior was not exhibited under the lack of visual targets in control experiments (N = 5 individuals). Older insects (6-day-old and 12-day-old) generally showed no jumping. They either climbed down the vertical rod or rested in a still posture on the platform after trying to reach out with forelegs.

3. Discussion

Canopy dispersal and evolution of gliding in *E. tiaratum*

The tactic use of gravity and environmental light gradient by newly hatched *E. tiaratum* supported our initial hypotheses on the fundamental roles of these two cues for legged movement in the canopy space, as found in locomotion in other ecosystems (e.g., larval insects, mites, and protists in oceanic ecosystems; Perkins et al., 2008; Zhang, 1992; Häder, 1987; Kamykowski et al., 1998). Their tactic movements toward vertically oriented contrast lines suggest a strategy for locating vertically oriented vegetational structures, especially stems, for accessing greater altitude. Specifically, the preference to dark surfaces, which correspond to dark or shaded areas in nature, may be a strategy for reducing the exposure to visual predators during dispersal. Similar preference was shown in gliding (Zeng et al., 2015). On the other hand, this preference corresponds to a high sensitivity under low environmental luminance (e.g., < 5 lx; **Fig. 3B**), which allows for greater visual acuity under low light. To further understand the cognitive behavioral process of dispersal in nymphal *E. tiaratum*, future studies may study their movements within environments of more complex visual signals and three-dimensional structures. Also, the potential use of other directional cues (e.g., polarized light, chromatic signals, chemical cues and humidity gradient) in the canopy space can be tested using binary choice experiments. Recording their movements on real vegetational structures (e.g., Lagrangian approach; Baguette et al., 2014) can provide direct observation on their integrative use of various short-range and long-range cues.

A multimodal movement strategy, consisting of both aerial and legged phases, can help small insects transport efficiently in canopy space. We predict that, under natural conditions, the dispersing *E. tiaratum* may frequently alternate movements on vegetational structures and in air, forming a behavior loop (**Fig. 8A**). An aerial phase may be initiated by missed landing, environmental perturbation and predatory attacks. After falling, the energy for re-ascending can be effectively saved by aerial righting and gliding. The self-dropping reflex that triggers the withdrawal of all tarsi may present a reflex arc similar to 'avoidance reflexes' at the single-leg level (Kittmann, 1996). Various mechanisms for foothold withdrawal may underlie different voluntary self-dropping mechanisms in phasmids (Bedford, 1978) and other insects (e.g., ants and aphids; Haemig, 1997; Humphreys and Ruxton, 2019).

In addition to the frequent initiation of aerial descent, the diurnal niche also plays a key role in the evolution of gliding in nymphal *E. tiaratum.* As the control of midair maneuvering and landing depend on the strength and continuity of vertically oriented contrast edges (e.g., tree trunks; Zeng et al., 2015), the quality of both decreases with lower light, a low light condition would obstruct gliding performance with low signal strength and low signal-to-noise ratio. Arthropods' compound eyes generally possess much lower acuity compared to vertebrate eyes (Land, 1997), thus more dependent on the visual contrast associated with tree trunks – which are most visible during daytime – for directed landing than vertebrates. Therefore, a diurnal niche may be critical to the evolution of arthropods' gliding in general, whereas less so with vertebrates. This is indirectly supported by the observation of diurnal gliding in various arthropods (Dudley and Yanoviak, 2011; Yanoviak et al., 2015) and nocturnal gliding in different vertebrate gliders (e.g., colugos; Byrnes et al., 2011), which demands more systematic comparison. To further understand the potential constraints of temporal niche on arthropod gliding, future studies can sample the visual appearance of vegetational structures across different heights during different times of the day, and evaluate the spatiotemporal variation of the visual quality of landing

targets. Also, comparing the spatiotemporal niches (e.g., active height and time on canopy) and the behavioral ecology of aerial descent initiation (e.g., defensive strategies and environmental perturbation) between arboreal invertebrates capable of gliding (e.g., arboreal insects and arachnids; Yanoviak et al., 2011; Yanoviak et al., 2015) may further reveal the common features in spatiotemporal niche shared among these taxa.

Evolution of diurnal dispersal in nymphal phasmids

Phasmids are generally nocturnal (Bedford, 1978). The diurnal hatching in *E. tiaratum* likely evolved under the selection for high dispersal efficiency in a rainforest ecosystem. The ascending dispersal of ground-hatched nymphs poses a transient spatial niche on vegetational structures, and life history traits may evolve to enable the best use of environmental cues for navigation and movement. As both environmental brightness and temperature are the strongest around midday (Shuttleworth, 1985), hatching around midday is more advantageous than any other time, as summarized in **Fig. 8B**. As associated with the disperser's syndrome, ant-mimicry (myrmecomorphy) in newly hatched *E. tiaratum* may help to defend against visual predators while moving on vegetational structures. Similar ant-mimicry phenotype is noted in newly hatched nymphs of several unrelated phasmid species (**Fig. 8C**; also, see Hanibeltz et al., 1995). These nymphs all ground-hatched and diurnally active. The independent evolution of this strategy implies a common demand for dispersal efficiency in species with transient spatial niche. The high abundance of nocturnally active predators on vegetational surfaces (Berger and Wirth, 2004) may also make diurnal dispersal safer. Future work can correlate different dispersal strategies (e.g., diurnal dispersal with ant-mimicry vs. nocturnal dispersal with camouflage) with oviposition style and habitat type to understand the evolution of diurnal dispersal in phasmids.

4. MATERIALS AND METHODS

4.1 Experimental insect husbandry

Eggs of *E. tiaratum* were incubated on vermiculate substratum with ~70% humidity under 25–27 °C. Newly hatched nymphs were collected every 12 hours and maintained in clear plastic cups (354 ml) with caps. Nymphs were provided with fresh leaves of Himalayan Blackberry (*Rubus armeniacus*) since the day of hatch, and was lightly sprayed with water every 2–3 days. Cups were kept in an environmentally controlled room with 12h:12h light : dark cycles and constant temperature (25–27°C). All experiments were conducted under 25–27°C.

4.2 Negative gravitaxis

A vertically oriented T-maze within a visually homologous chamber was used. A T-shaped system of wooden rods (diameter, 9 mm) was placed in the center of a chamber (40×40×40 cm), which was covered with white felt and surrounded by natural-spectrum bulbs (R30FF100VLX, Verilux Inc., VT, USA) with voltage control (**Fig. 2A**). The environmental luminances at the center of the chamber was measured with a lightmeter (401025, Extech, MA, USA; spectral range: 400–740 nm). In each trial, the experimenter first released the insect through the entrance window and then observed the insect's directional choice through observation window. A minimum of 3 minutes was given between trials. Experiments were conducted for three age groups (0–1, 6–7, and 12–14 day-old) under four environmental luminances (0 lx, 10 lx, 600 lx, 1.5×10^4 lx). Each combination of age and luminance was tested with 10–26 individuals (4–6 trials per individual). Repeated G-test (McDonald, 2015) was used to test the frequencies of negative gravitaxis ($f_{ascending}$) against the null frequency of 50%. Poisson GLMM was used to test whether the counts of ascending response were significantly correlated with environmental luminance and age, with individuals as random factors.

4.3 Phototaxis

A T-maze was used to test the insects' phototactic response. The T-maze consisted of two tunnel sections (section 1: diameter 2 cm, length 20 cm; section 2: diameter 4.5 cm, length 10 cm), and the inside of both sections were covered with black fabric to reduce light reflection (**Fig. 3A**). A natural-spectrum bulb (R30FF100VLX, Verilux Inc., VT, USA) with voltage controller was placed ~5 cm away from each exit of the T-maze, with a paper screen (5×5 cm) positioned 3 cm away from each exit. Luminance was measured with a light meter (401025, Extech, MA, USA; spectral range: 400–740 nm) at two exits. Three luminance gradients (0 lx vs. 3 lx, 100 lx vs. 500 lx, and 10000 lx vs. 20000 lx) were tested, which range covers the luminance variation between forest understories and canopies (e.g., ~600 lx to 2.4×10^4 lx; Bjorkman and Ludlow, 1972; Pearcy, 1983; Lee, 1987). Each luminance gradient was tested in insects of three ages (0–1 day-old, 5-day-old, and 10-day-old), each represented by 5–20 individuals (5–6 trials per individual). During each trial, the experimenter first released the insect into the entrance, immediately covered the entrance with a lid and then recorded the insect's directional choice within the light gradient. The control experiments were conducted in one 0–1 day-old group in complete darkness, and an infrared video camera (SONY HDR-HC7) was used to observe the insects' directional choice. Repeated G-test was used to analyze the significance of directional bias against the null frequencies (1:1). Poisson generalized linear mixed models (GLMM) were used to test the

correlation between the counts of phototaxic responses and environmental luminance, for which individuals were set as random factors.

4.4 Tactic responses to visual contrasts

The insects' directional choices were examined using a cylindrical arena (height 35 cm, diameter 26 cm) internally decorated with vertically oriented contrast patterns. The patterns were made with felt sheets in black, gray and white (average reflectance over 300–550 nm: black, 3%; gray, 38%; white, 47%; measured by a spectrophotometer, USB2000, Ocean Optics, Dunedin, FL, USA; see Zeng *et al.*, 2015). A natural spectrum light bulb (R30FF75VLX, Verilux Inc., VT, USA) was set atop the arena and provide ~600 lx luminance at the arena floor (measured with a light meter, Extech 401025, Waltham, MA, USA) (**Fig. 4A**).

Five contrast patterns were used to test the insects' directional preferences to contrast strength and stripe size. The patterns formed by black and white surfaces were coded as BW11, BW91 and BW19, whereby the embedded numbers represent the relative proportions of black (B) and white (W) surfaces. In BW91 and BW19, the narrow stripes feature a spatial frequency of ~3.18 cyc/rad (as viewed from arena center). Similarly, two patterns formed by gray surfaces pairing with black or white surfaces in equal proportions were coded as BG11 and GW11. The effect of contrast strength to the insects' tactic response was tested using BW11, BG11, and GW11, and the effect of stripe size was tested using BW11, BW19 and BW91. Each contrast pattern was tested in 19–38 individuals (5 trials per individual).

In each trial, the insect was released through an entrance (diameter 2 cm) at the center of the arena floor and observed from above. Three temporal landmarks were recorded: (1) entrance into the arena, (2) reaching the arena wall, and (3) initiation of ascending. The insect's directional preference was represented by the angular distance between the point where the insect first reached the arena wall and the nearest contrast edge. The circular directionality of the insects' directional choice was analyzed using 'CircStats' package, which calculates the means and confidence intervals of direction θ and concentration κ based on von Mises Maximum Likelihood Estimates (Lund and Agostinelli, 2007). Repeated G-test was used to test the directional preference for the darker and the lighter surfaces for each setup against the null proportions, which were derived based on random drift and predicted the frequencies of choice were the same as area proportions of the surfaces. The time expenditures between temporal landmarks and the average speed of movement on arena floor were compared using repeated-measures ANOVA.

4.5 Ontogenetic decline of ascending endurance

We recorded the ascending movements of insects moving on a vertically oriented treadmill (width 2 cm, height 28 cm), which was connected to a speed controller and set in a dark room (**Fig. 5A**). A light source was placed above the treadmill to motivate the insects. A disc with visual marks was attached to the top shaft as a reference of treadmill speed. The insect and treadmill were filmed using a digital video camera (25 fps; HDR-XR160, Sony Corporation, Japan) in lateral view. For each trial, the experimenter first released the insect onto the track and then maintain the insects' position in video frame by manually adjusting the track speed. Nymphs of six ages were used (2, 4, 48, 96, 120, and 240 hour-old; see Supplementary Table S3), each filmed for 60 min. A motion tracking software (ProAnalyst, Xcitex,

MA, USA) was used to track the insects' instantaneous position and the orientation of the reference plate. Custom-written MatLab scripts were used to calculate the ascending speed as a function of time.

4.6 Self-dropping behaviors

Simulated predatory attacks and accidental loss of foothold were applied to experimental insects ascending on a vertically oriented cardboard (width, 15 cm; height, 35 cm) below a light source. Experimental insects were first released near the bottom of the board and allowed to ascend under phototaxis and negative gravitaxis. To simulate predatory attacks, a roll of paper towel (diameter ~5 mm) was used to press the insect's tibial and tarsal segments, confining the targeted leg against the substrate for ~20 ms without causing any injury (**Fig. 6A**; **Movie S3**). The experiment was conducted in three age groups (0-day-old, 6-day-old, and 12-day-old), with 10 –15 individuals per group. Each individual was tested in five trials; in each trial, each leg pair received two simulated attacks, with 10 sec between consecutive attacks. To induce accidental losses of foothold, a slippery surface (TEFLON-coated; ~2 cm wide) was introduced to the card board (**Fig. 6C**). The insects' response to touching the slippery surface was recorded in three age groups (0-day-old, 5-day-old and 10-day-old), with 7 individuals per group.

4.7 Jumping behavior for crossing air gaps

We tested the insects' jumping behavior by introducing them to an elevated platform (2 cm × 5 cm), which was mounted atop a vertically oriented rod and was ~50 cm above the floor and > 40 cm away from the walls. The floor and walls were covered with white felt, and the environmental luminance was ~600 lx. Two landing targets were used: (1) A horizontally oriented rod (diameter 5 mm) wrapped with black felt and positioned 20 cm below the platform, with a white background ~30 cm below the platform (**Fig. 6A**); (2) A vertically oriented rod, also wrapped with black felt, positioned ~8 cm away from the platform (**Fig. 6A**). For each setup, jumping behavior was tested in three age groups: 0-day-old, 6-day-old, and 12-day-old (horizontal target, 6–9 individuals per age group, 5 trials per individual; vertical target, 5–9 individuals per age group, 2–4 trials per individual). In each trial, the experimenter released the insect to the vertical rod and then observed its response for ~4 min after it reached the platform. If the insect stopped moving and changed to a camouflage posture, the experimenter would gently tap the vertical rod to stimulate the insect. A minimum of 2 min resting period was provided between trials. Control experiment was conducted in five 0-day-old individuals following the same protocols but without any visual target.

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Author contributions

Y.Z. devised the experiments. S.C., J.W., L.N., J.T. and G.N. participated in data collection and data analyses. All authors contributed to writing the manuscript.

Supplementary Movies

S1 – Newly hatched *E. tiaratum* nymphs dispersing with ant-mimicking coloration and movement.
S2 – An example trial of a *E. tiaratum* nymph navigating within the visual arena with visual contrasts.
S3 – Self-dropping reflex after a simulated attack, shown in slow motion (5X slowed based on original video filmed at 500 fps).
S4 – Self-dropping reflex after stepping on TEFLON-coated slippery surface.
S5 – Sample trials of jumping behavior for crossing air gaps.

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Figure captions

Figure 1. Post-hatch dispersal in *E. tiaratum*. (A) (Left) Natural habitat of *E. tiaratum*, showing the spatial complexity and vertically varying light environment. Photo was taken at lowland mesophyll forest, Polly Creek, Garradunga, Queensland, Australia (courtesy of Jack W. Hasenpusch). (Right) A schematic summary of *E. tiaratum* life cycle, showing the transient spatial niche in newly hatched nymphs, which ascend from forest floor to tree canopies. (B) The loss of ant-mimicking coloration during the first 3 – 5 days after hatching. (C) Two main categories of questions in this study, as structured following the 'movement ecology paradigm' (Nathan et al., 2008).

Figure 2. Nymphal *E. tiaratum* exhibited negative gravitaxis under various environmental luminances. (A) Schematic demonstration of the experimental setup. A vertically oriented T-maze made of two rods installed within a cubic chamber covered with white felt, surrounded by voltage-controlled light bulbs for homogeneous luminance (Right). An entrance (2×2 cm) on the chamber wall was opened for the horizontal portion of the T-maze, and an observational window (2×2 cm) was opened at the chamber top. Experimenter first released the insect to the terminal of the horizontal rod (Step 1) and then observed the directional choice of the insect (Step 2). (B) Ascending frequency (f_g) versus age under various environmental luminances. An ontogenetic decline of ascending frequency was found in total darkness (0 lx). Values are means ± s.e.m. All frequencies are significantly different from the null predictions ($P < 0.001$, repeated G-test). See Methods for sample size.

Figure 3. Nymphal *E. tiaratum* exhibited positive phototaxis. (A) A schematic demonstration of the experimental setup in dark room. A T-maze made of two dark tunnels with a luminance gradient at the intersection. In experiment, the experimenter first released the insect at the entrance (Step 1) and then recorded its directional choice within the luminance gradient (Step 2). (B) Ontogenetic variation of phototaxis response under different luminance gradients. Values are frequencies of phototaxic movements (f_p; means ± s.e.m.). Asterisk symbols denote significance level of results based on repeated G-test: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. In old nymphs, the frequency of phototaxic response was inversely correlated with the average luminance (5-day-old, $P < 0.05$; 10-day-old, $P < 0.01$; Poisson GLMM). See Methods for sample size.

Figure 4. Newly hatched nymphal *E. tiaratum* are attracted by vertically oriented visual contrasts. (A) A schematic illustration of visual arena, the inner wall of which showed different contrast patterns (see Methods). Experimenter first released the insect to the arena entrance (Step 1) and then observed its behavior until reaching the arena wall (Step 2). (B)-(C) Summary of directional choice for contrasts formed between surfaces of equal size. Subplots in (B) summarizes the directional preference with respect to the contrast edge, with histograms showing the distributions of movement direction. Insets are schematic diagrams of the visual arena in top view, with the red sectors showing the plotted angular range. Red dot denotes mean angular position with error bars showing 10th and 90th percentiles. The movement direction exhibited the greatest concentration with black-gray contrast, as shown by a comparison of the concentration parameter κ (means±95% CI) in (C). (D) A comparison of mean speed of insects' movement toward arena wall with different contrast patterns. The insects moved with the fastest speed when exposed to black-gray contrast. Values are significantly different between trials ($F_{2,27} = 5.09$, $P < 0.05$, repeated-measures ANOVA). (E) A comparison of ascent initiation time (the period between reaching the arena wall and initiating ascent) with different contrast patterns. The insects exhibited a significant delay when exposed to gray-white contrast. Values are significantly different between trials ($F_{2,27} = 3.43$, $P < 0.05$, repeated-measures ANOVA). For (D) and (E), values are means±s.e.m. (F)-(G) Summary of directional choice for contrasts formed between surfaces of different sizes. The insects exhibited preference to the narrower surface regardless of its brightness, as shown by the significantly greater frequencies than the null (G). For (D) and (F), the number of experimental insects and trials were shown in parentheses. Also, see **movie S2** and **Supplementary Table S1-S2**.

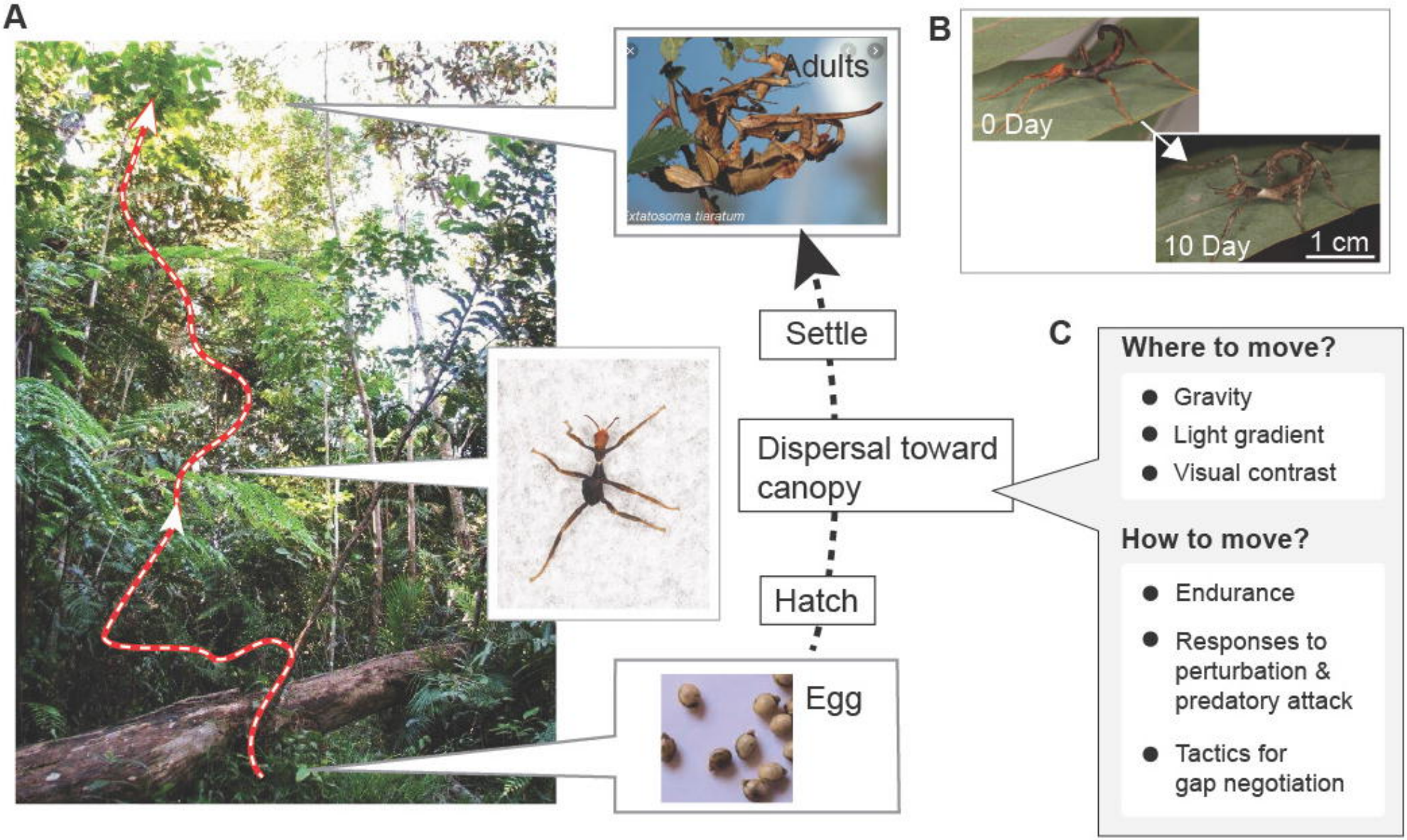
See Methods for sample size.

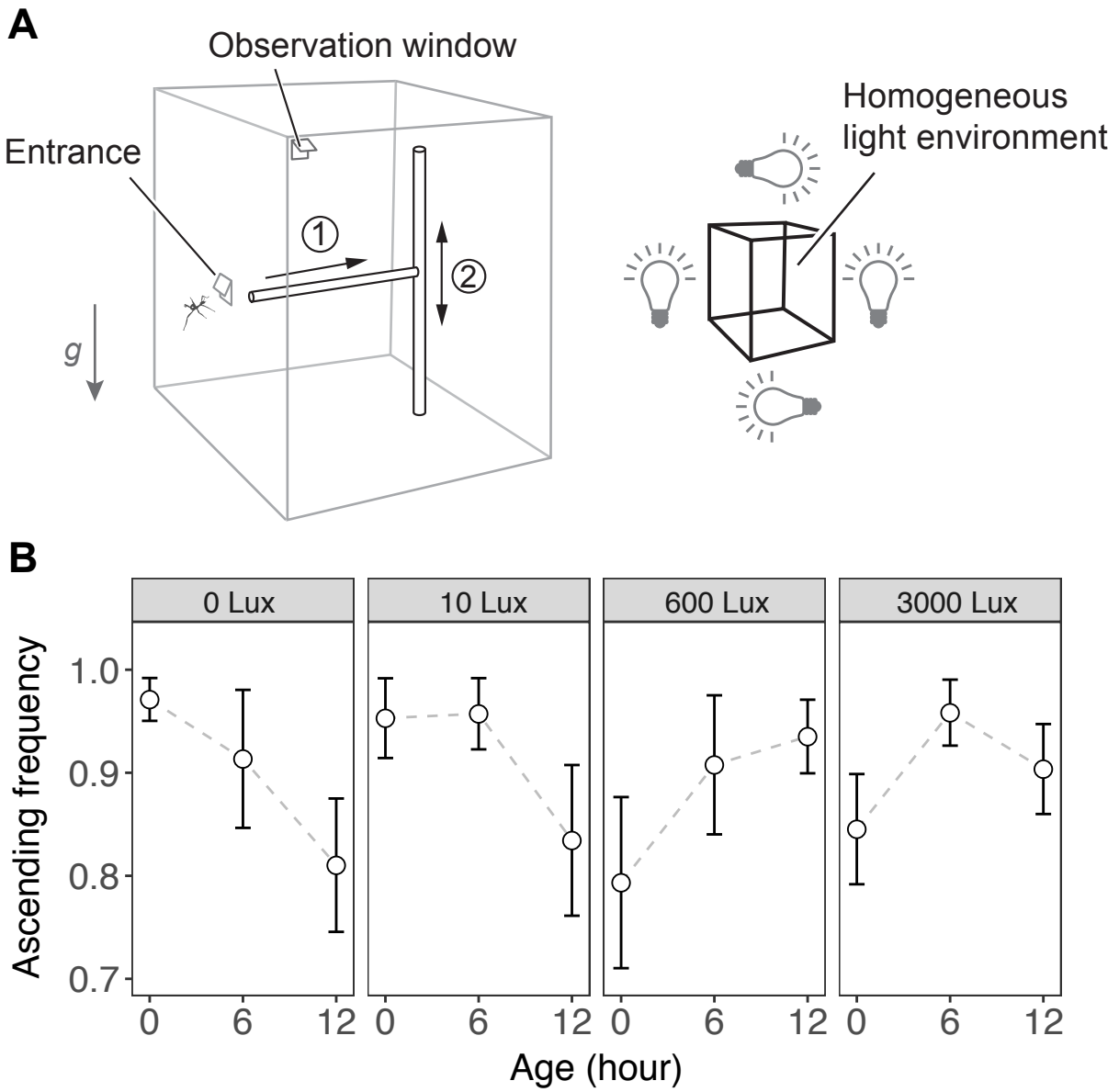
Figure 5. The ontogeny of ascending behavior in nymphal *E. tiaratum*. (A) Schematic demonstration of experimental setup, a vertically oriented treadmill with a light source on the top. The ascending insect was maintained in the camera view through manual speed control by the experimenter. (B) A sample of the insect's speed profile, showing active ascending movements with intermittent pauses. (C) Ontogenetic variation of the speed of ascending. The mean ascending speeds are significantly different between age groups ($F_{5,20}$ = 18.4, P<0.001, One-way ANOVA). (D) The temporal percentage of active ascending relative to the total (60 min), showing a sharp reduction after 2-hr. Inset shows significantly greater frequency of pausing in the newly hatched nymphs (2-hr) than older. (E) A comparison of total ascent height within 60 min between different age groups, with significant inter-group differences ($F_{5,18}$ = 6.14, P<0.01, One-way ANOVA). For (B)-(E), values are means±s.d. Also, see **Supplementary Table S3**.

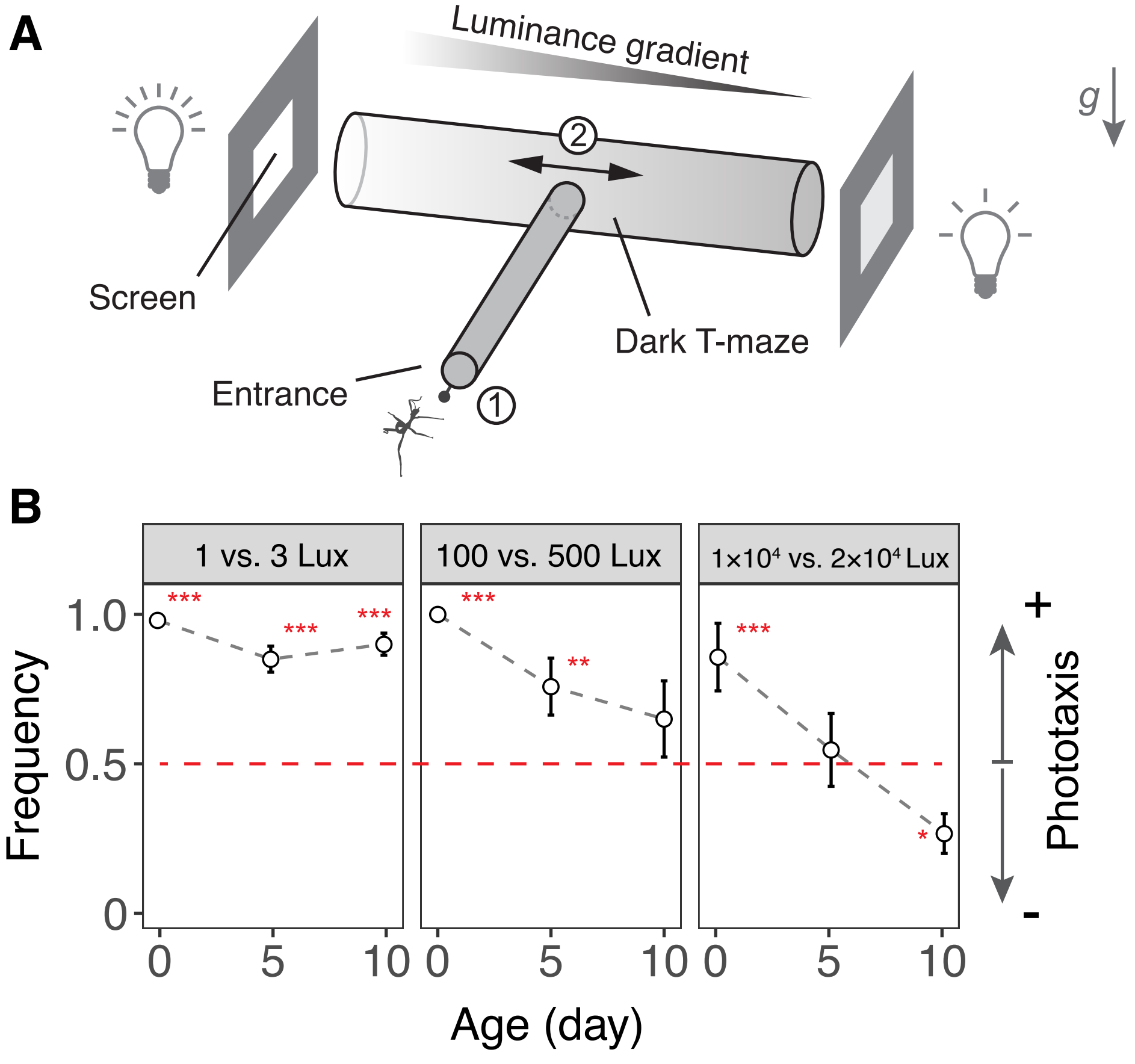
Figure 6. Newly hatched *E. tiaratum* initiate self-drop under tactile stimulations. (A) A high-speed video sequence of self-dropping initiation in response to simulated predatory attack. (B) Newly hatched nymphs showed significantly higher frequency of self-dropping after simulated attacks. Values are means±s.e.m. (0-day-old, N = 14 individuals, N = 124 trials per leg pair; 6-day-old, N = 22 insects, N = 208 trials per leg pair; 12-day-old, N = 10 insects, N = 100 per leg pair). Also, see **Movie S3**. (C) A sample sequence of self-dropping in response to sudden loss of foothold by touching a slippery surface. Inset shows experimental setup. (D) Newly hatched nymphs showed significant higher frequency of self-dropping after sudden loss of foothold. Values are means±s.e.m. (0-day-old, N = 7 insects, N = 59 trials; 5-day-old, N = 7 insects, N = 50 trials; 10-day-old, N = 7 insects, N = 50 trials). Also, see **Movie S4**.

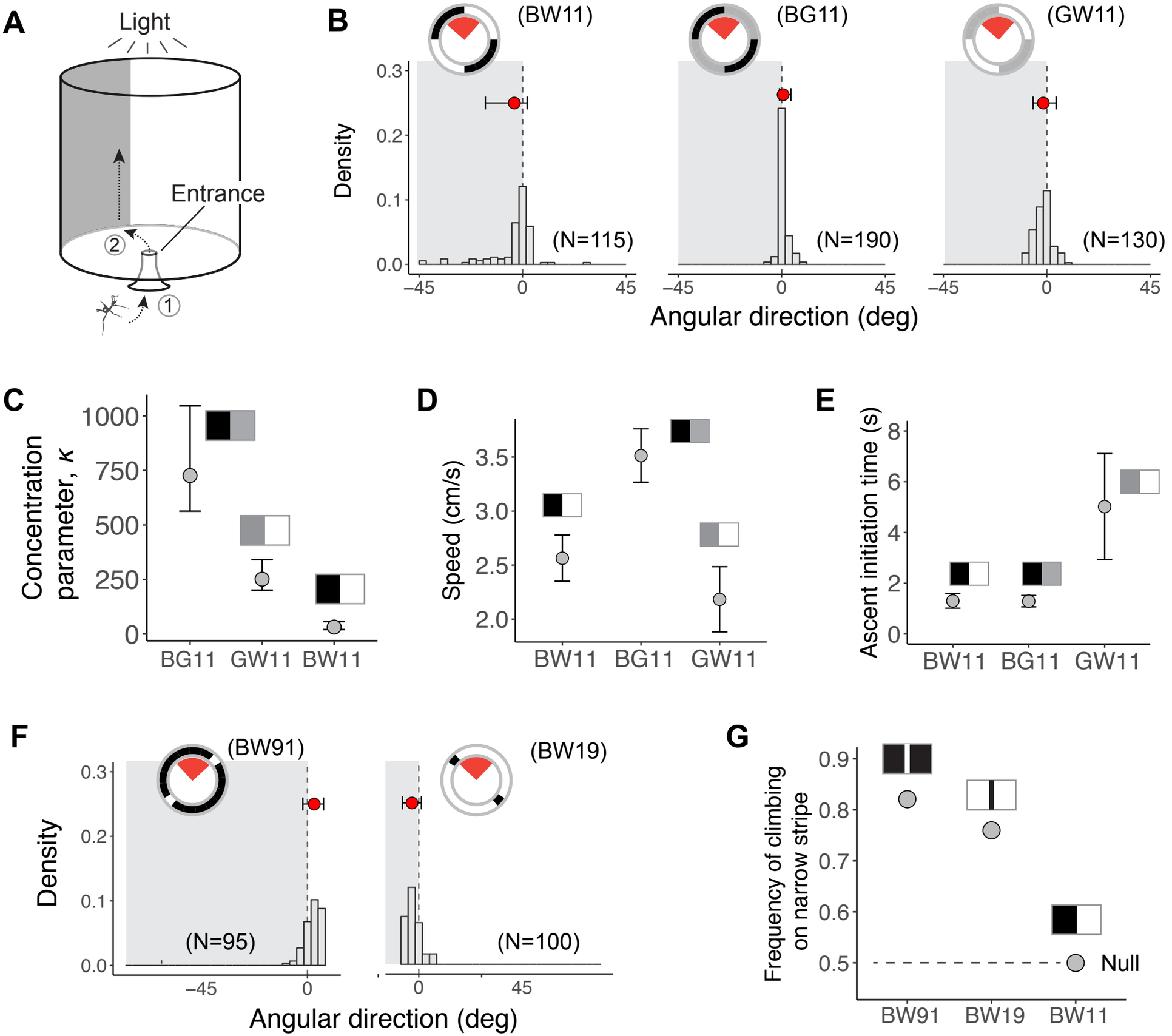
Fig. 7. Newly hatched *E. tiaratum* jump to cross air gaps. (A) Two experimental setups. In each trial, the experimental insect first ascent to the jumping platform through a vertical wooden rod (Step 1), and its subsequent response to a distant land target (dark rod with a white background) was recorded (Step 2). Inset shows the general behavioral sequence. (B) The variation of jumping frequency versus age of the insects, showing significant ontogenetic reductions of jumping behavior. Values are means±s.e.m. See Results for statistical summary. Also, see **Movie S5**.

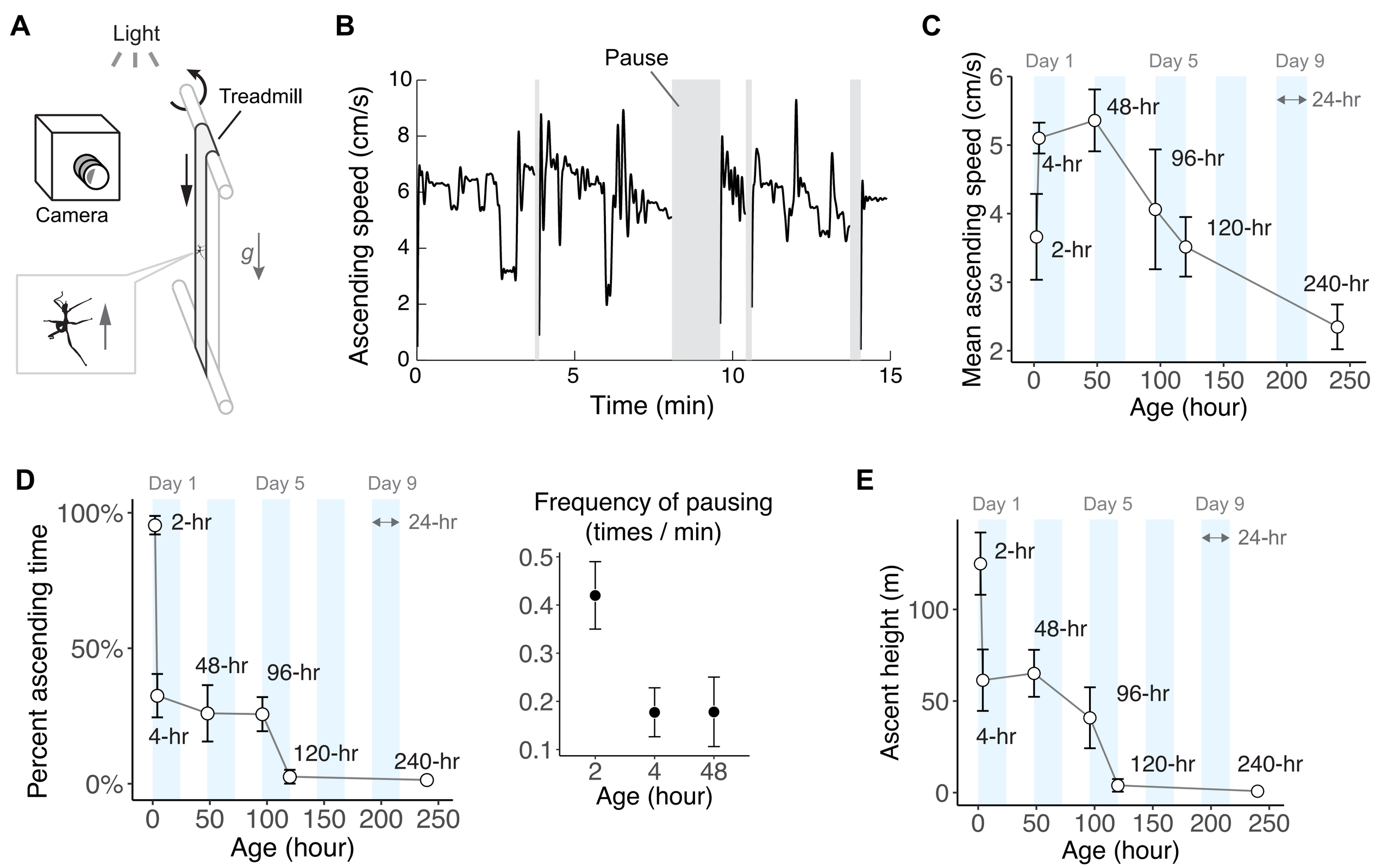
Figure 8. Ecology and evolution of diurnal dispersal in newly hatched stick insects. (A) Navigation and movement processes of post-hatch dispersal in *E. tiaratum* (top; following 'movement ecology paradigm'; Nathan et al., 2008), where the alternation between movements on vegetational structures and in air form a behavioral loop (bottom left), as shown by a schematic demonstration (bottom right). (B) The diurnal dispersal in nymphal *E. tiaratum* is likely an evolutionary consequence to the interplay between (1) an obligatory transient spatial niche and (2) a diurnal temporal niche for greater dispersal efficiency. (C) Examples of newly hatched first phasmid nymphs (from different families) that are ground-hatched and diurnally-active with ant-mimicking coloration and behavior. (i) *Podacanthus* sp. (Phasmatidae) from Queensland, Australia (photo courtesy of Tony Eales); (ii) *Phyllium philippinicum* (Phylliidae) from Philippines; (iii) *Paraprisopus* sp. (Prisopodidae) from Panama (photo courtesy of Bruno Kneubu□hler); (iv) *Orthomeria* sp. (Aschiphasmatidae) from Sarawak, Borneo (photo courtesy of Bruno Kneubu□hler).

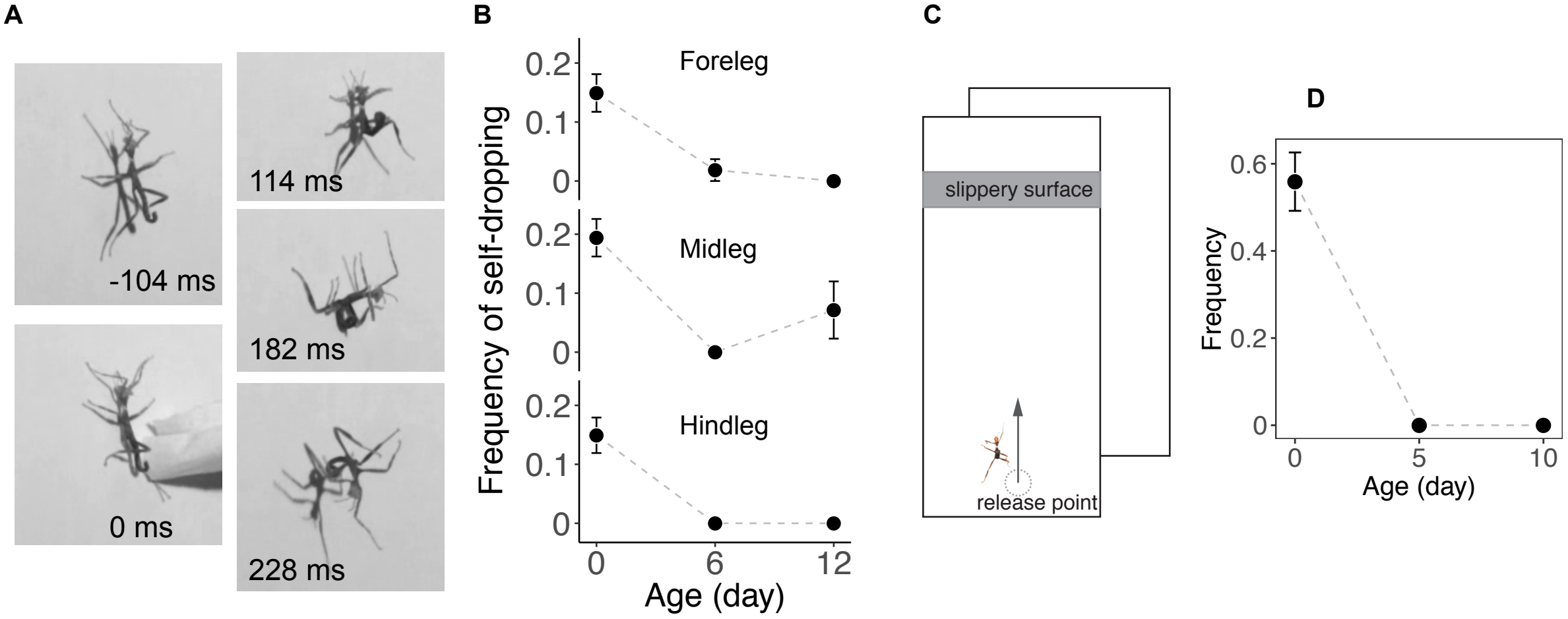

A
Adults
xtatosoma tiaratum
B
0 Day
10 Day
1 cm
Settle
Dispersal toward canopy
Hatch
Egg
C
Where to move?
Gravity
Light gradient
Visual contrast
How to move?
Endurance
Responses to perturbation & predatory attack
Tactics for gap negotiation

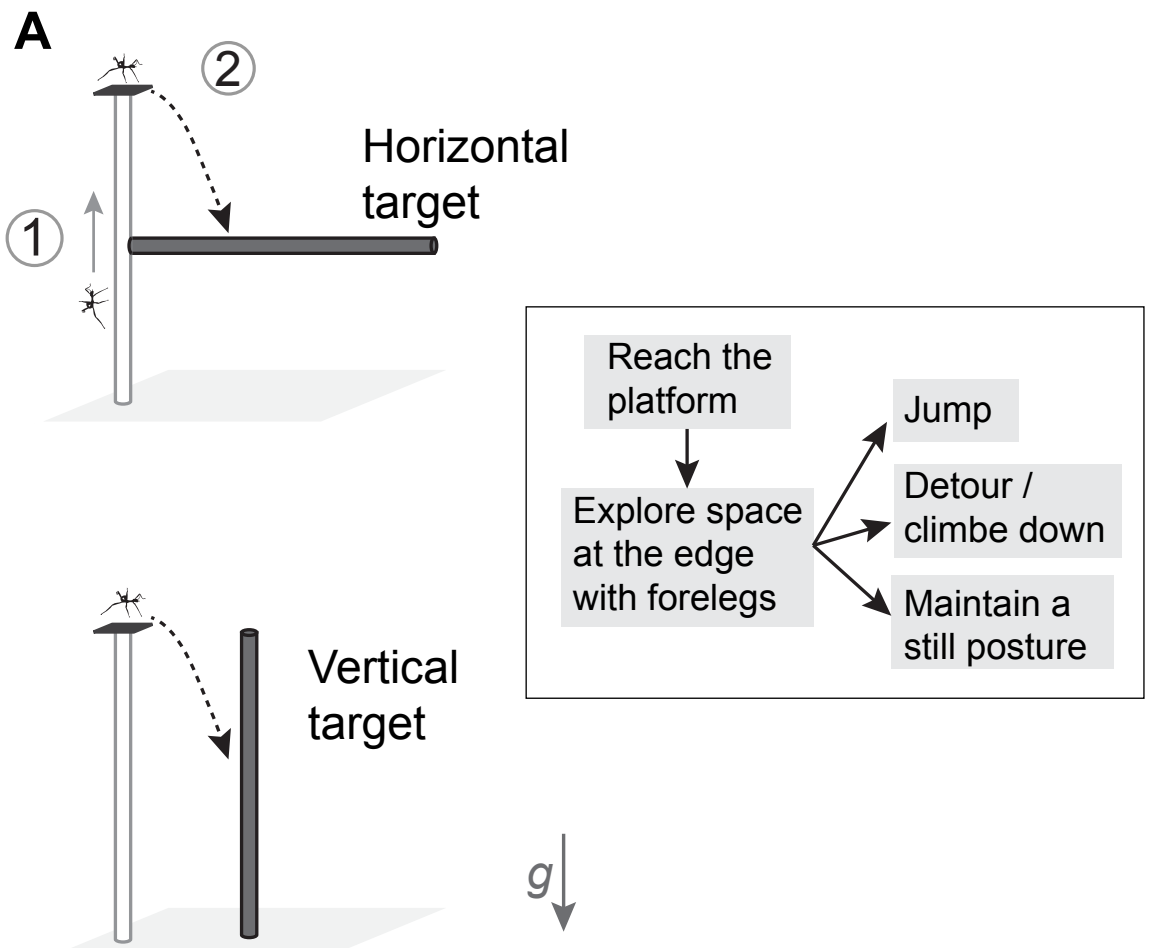

A
Observation window
Entrance
①
②
g
Homogeneous
light environment
B
0 Lux
10 Lux
600 Lux
3000 Lux
Ascending frequency
1.0
0.9
0.8
0.7
0
6
12
Age (hour)

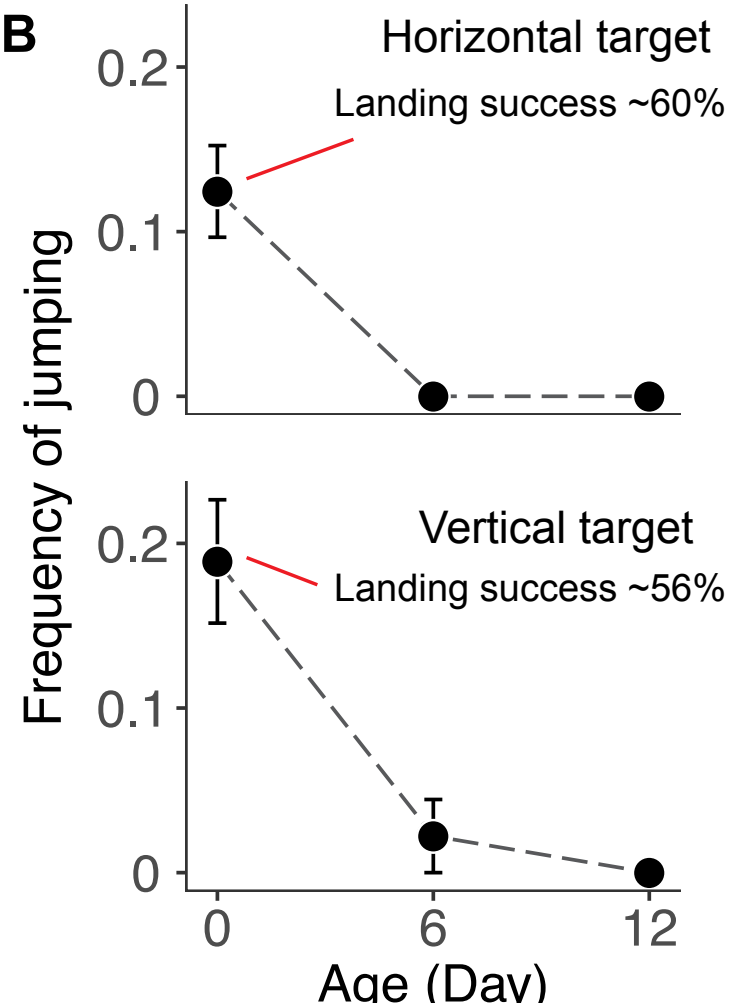

A
Luminance gradient
g
2
Screen
Dark T-maze
Entrance
1
B
1 vs. 3 Lux
100 vs. 500 Lux
1×10⁴ vs. 2×10⁴ Lux
Frequency
1.0
0.5
0
***
***
***
***
**
***
*
0
5
10
Age (day)
+
-
Phototaxis

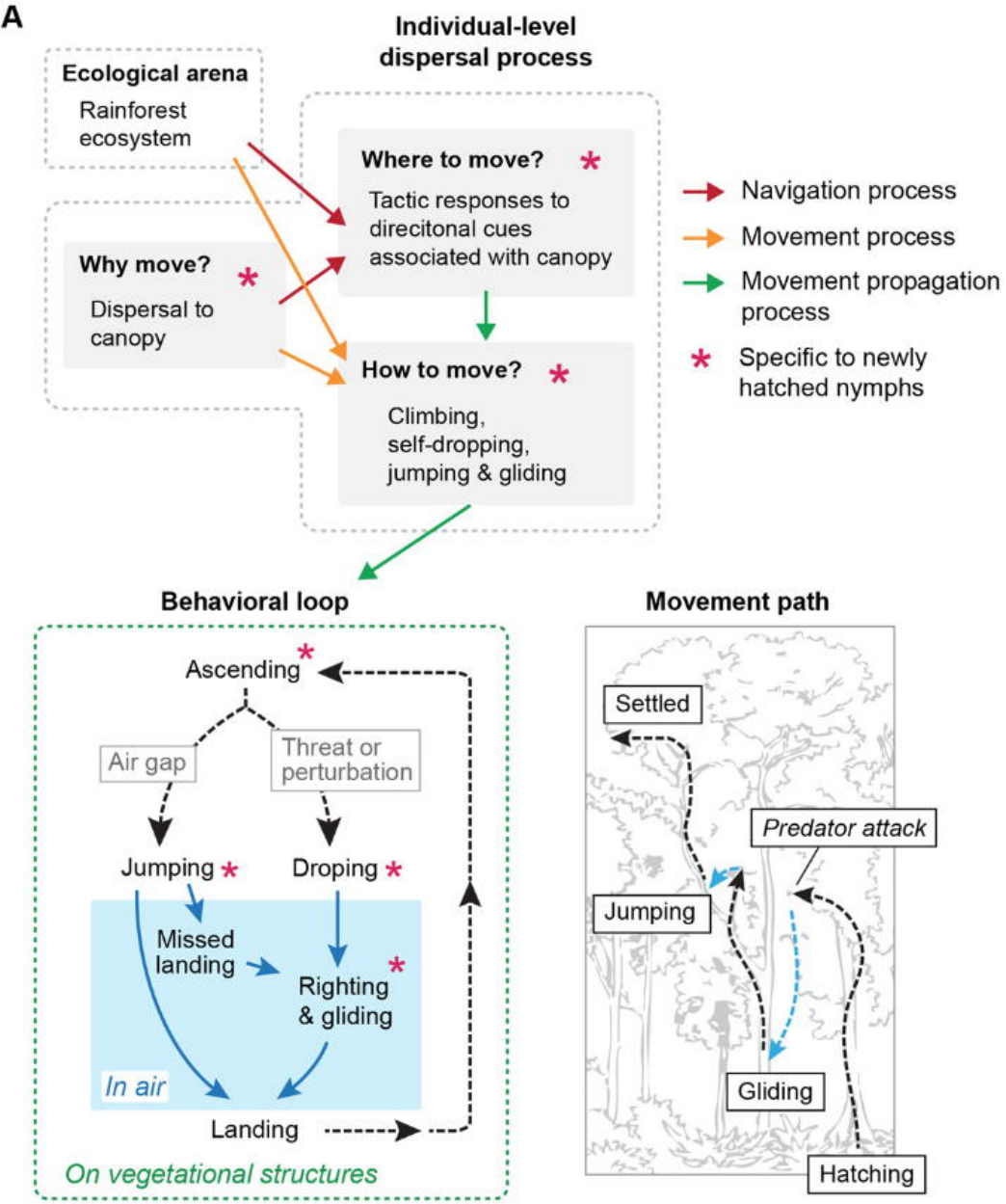

A
Light
Entrance
②
①
B
(BW11)
(BG11)
(GW11)
Density
0.3
0.2
0.1
0.0
(N=115)
(N=190)
(N=130)
−45
0
45
Angular direction (deg)
C
Concentration parameter, κ
1000
750
500
250
0
BG11
GW11
BW11
D
Speed (cm/s)
3.5
3.0
2.5
2.0
BW11
BG11
GW11
E
Ascent initiation time (s)
8
6
4
2
0
BW11
BG11
GW11
F
(BW91)
(BW19)
Density
0.3
0.2
0.1
0.0
(N=95)
(N=100)
−45
0
0
45
Angular direction (deg)
G
Frequency of climbing on narrow stripe
0.9
0.8
0.7
0.6
0.5
Null
BW91
BW19
BW11


A
Light
Treadmill
Camera
g
B
Pause
Ascending speed (cm/s)
Time (min)
C
Day 1
Day 5
Day 9
24-hr
Mean ascending speed (cm/s)
Age (hour)
2-hr
4-hr
48-hr
96-hr
120-hr
240-hr
D
Percent ascending time
Frequency of pausing
(times / min)
E
Ascent height (m)


A
-104 ms
114 ms
182 ms
0 ms
228 ms
B
Foreleg
Midleg
Hindleg
Frequency of self-dropping
0.2
0.1
0
0
6
12
Age (day)
C
slippery surface
release point
D
Frequency
0.6
0.4
0.2
0
0
5
10
Age (day)


A
2
1
Horizontal target
Vertical target
Reach the platform
Explore space at the edge with forelegs
Jump
Detour / climbe down
Maintain a still posture
g


B
Horizontal target
Landing success ~60%
Vertical target
Landing success ~56%
Frequency of jumping
0.2
0.1
0
0
6
12
Age (Day)



B

Life history

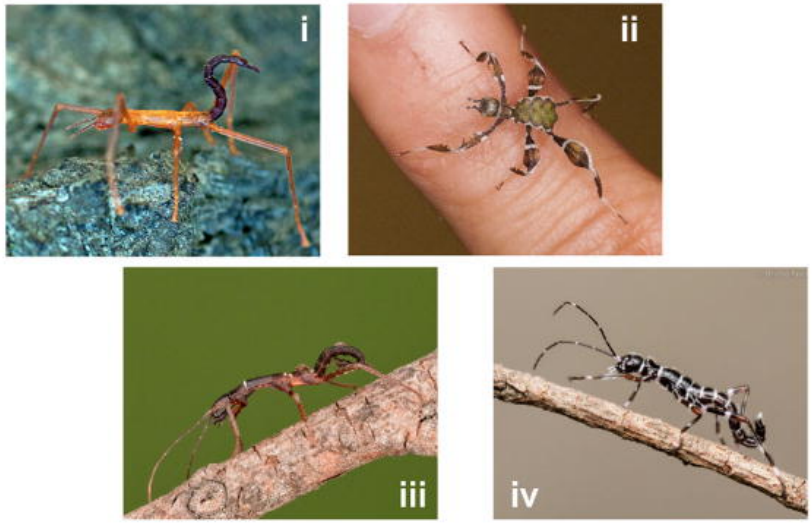
Ground-hatching & arboreal-dwelling

Ecosystem

	Night	Day
Visual signal	- weak	- strong
Temperature	- low	- high

Transient spatial niche from forest floor to canopy + Higher dispersal efficiency during the daytime

Diurnal post-hatch dispersal

Trait	Adaptive significance
Use of gravitational and visual cues	Efficient navigation and directed dispersal
High endurance	Sustained exploration and long-distance travel
Ant-mimicry	Defend visual predators

C