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Prolonged Moderate-intensity Light Exposure Alters Phototaxis in the Acoel Flatworm (*Praesagittifera naikaiensis*)

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Many animal behaviors are executed with appropriate form, direction, and intensity in accordance with an individual's physiological state and its history of interactions with the environment. Although taxis has long provided a useful framework for describing stimulus-guided orientation, contemporary work has shown that such responses are mechanistically diverse and can involve more than simple automatic approach or avoidance. Here, we examined whether phototaxis in the acoel flatworm (*Praesagittifera naikaiensis*) undergoes experience-dependent modification. We conducted three experiments. First, we tested whether prior light exposure for 1 to 5 days attenuates phototaxis. A prolonged light exposure weakened phototactic attraction. This attenuation, however, could reflect general debilitation caused by light exposure. We therefore assessed in Experiment 2 whether five days of light exposure reduces spontaneous locomotor activity. No such reduction was detected. In Experiment 3, we placed *P. naikaiensis* on a platform containing a continuously illuminated region and a shaded region for five days, and asked whether prolonged exposure would induce spontaneous light avoidance. The worms were attracted to light for approximately the first 24 hours, after which they tended to avoid light and moved into the shaded region. These results indicate that phototaxis in *P. naikaiensis* is adaptively tuned to the individual's history of light exposure.

Keywords: acoelomorpha, behavioral flexibility, phototaxis

長時間の中強度光曝露は無腸動物（ナイカイムチョウウズムシ *Praesagittifera naikaiensi*）の光走性を変容させる

多くの動物の行動は、個体の生理的状態および環境との相互作用の履歴に応じた、適切な様式、方向、強度で実行される。走性は刺激誘導性の定位行動を記述するうえで、長い間有用なフレームワークを提供してきたが、最近の研究ではこうした反応がメカニズム的に多様であり、単なる自動的な接近・忌避以上のものを含んでいることが示されている。本研究では、無腸動物（ナイカイムチョウウズムシ *P. naikaiensis*）における光走性が、経験依存型の変調を受けるかを調査した。我々は 3 つの実験を実施した。まず我々は、1〜5 日間の事前光曝露が、光走性を減衰させるかをテストした。長期間の光への曝露は光走性における誘引を弱めた。しかしこの減衰は、光への曝露によって起きる全般的な機能低下を反映している可能性があった。そのため実験 2 において、5 日間の光曝露が自発的な運動活性を減少させるかを評価した。その結果、そのような減少は見られなかった。実験 3 において、*P. naikaiensis* を持続的に照明された領域と、遮光された領域を含むプラットホームに 5 日間配置し、長時間の曝露が自発的な光忌避を引き起こすかを調べた。供試個体は、最初の約 24 時間は光に誘引されたが、それ以降は光を避ける傾向を示し、遮光領域へと移動した。これらの結果は、*P. naikaiensis* における光走性が個体の光曝露の履歴によって適応的に調整されることを示している。

キーワード：無腸動物、行動柔軟性、光走性

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La exposición prolongada a luz de intensidad moderada altera la fototaxis en el gusano plano acoelo (*Praesagittifera naikaiensis*)

Muchos comportamientos en animales se expresan con una forma, dirección e intensidad acordes con el estado fisiológico del individuo y con su historial de interacciones con el ambiente. Aunque el concepto de taxia ha constituido durante largo tiempo un marco útil para describir la orientación guiada por estímulos, estudios recientes han mostrado que estas respuestas presentan una considerable diversidad mecanística y pueden involucrar algo más que un simple acercamiento o alejamiento automáticos. En el presente estudio se evaluó si la fototaxis del gusano plano acoelo (Praesagittifera naikaiensis) puede modularse en función de la experiencia previa. Se realizaron tres experimentos. En el primero, se evaluó si la exposición previa a la luz durante períodos de entre uno y cinco días atenuaba la respuesta fototáctica. La exposición prolongada a la luz redujo la atracción fototáctica. Sin embargo, esta disminución podría atribuirse a un deterioro general provocado por la exposición a la luz. Por ello, en el segundo experimento se examinó si cinco días de exposición lumínica reducían la actividad locomotora espontánea. No se detectó ninguna disminución de dicha actividad. En el tercer experimento, los individuos de *P. naikaiensis* se mantuvieron durante cinco días sobre una plataforma con una región iluminada de forma continua y otra sombreada, con el fin de determinar si la exposición prolongada inducía una evitación espontánea de la luz. Durante aproximadamente las primeras 24 horas, los gusanos mostraron una respuesta de atracción hacia la luz; posteriormente, tendieron a evitarla y se desplazaron hacia la región sombreada. En conjunto, estos resultados indican que la fototaxis en *P. naikaiensis* se ajusta de manera adaptativa en función del historial individual de exposición a la luz.

Palabras clave: Acoelomorpha, flexibilidad conductual, fototaxis

Behavior is not governed solely by the current environment; it is appropriately adjusted by an organism's history of interactions and by the physiological states that arise from that history. This is evident in everyday life: what counts as a reward is determined by an individual's physiological state (e.g., food functions as a reward depending on hunger). Recent formulations of reinforcement learning locate the origin of reward in the monitoring of internal states (Weber et al., 2025). Indeed, the dependence of behavior on experience and internal state has been demonstrated across numerous behavioral phenomena and taxa.

Indeed, behaviors that appear instinctive and mechanical can exhibit fine-grained adjustment. Classically, Charles Darwin reported that the effort earthworms invest in plugging the entrances to their burrows varies with ambient dryness (Darwin, 1892). When the air is humid, the plug may be "rough" without risking desiccation, indicating that worms adjust their actions to maintain physiological condition in accordance with environmental circumstances (Reed, 1982). In crayfish, the tail-flip escape response is rapid and reflex-like, yet the lateral giant neuron that controls this response is suppressed during feeding, which elevates the response threshold (Krasne & Lee, 1988).

How widely across evolution are such state-dependent mechanisms of behavioral adjustment distributed? It is important to investigate species across diverse animal lineages that retain relatively basal traits (Lyon & Cheng, 2023). Certainly, long before humans evolved their highly flexible forms of behavior, organisms presumably had already developed biological functions for sensing, responding to, and adjusting to the external world, providing a basis from which more elaborate forms of adaptive behavior could arise in other lineages. Likewise, Charles Darwin's observations of earthworms indicate that such behavior is not a trivial reflex.

Investigating the extent to which, and the behavioral domains in which, the plasticity or modifiability of natural behaviors that appear "instinctive" at first glance extends across taxa is a task for comparative psychology (cf. Matsui & Hata, 2025a). Across classical and contemporary accounts, taxis has been regarded as a reflexive form of behavior (Giraldo et al., 2018; Parmelee, 1913). For example, Pisula (2016) writes, "Taxis is a stereotyped response to a specific stimulus. The organism acts like an automaton." Phototaxis, in particular, appears to involve attraction to a clearly defined stimulus (light) and thus to present as a fixed mode of movement. Yet, several studies have reported plastic modulation even in taxis. In Drosophila, the sign of phototaxis changes with flight capability (Gorostiza et al., 2016). Planarians that exhibit negative phototaxis show long term habituation to light (Prados et al., 2020). Taken together, these studies indicate that behaviors that seem mechanical and reflexive can, in fact, be flexibly controlled by internal state and experience.

Thus, the classical concept of taxis was originally used to describe the behavior of "simple" animals as largely automatic, and this view has continued to influence the field. However, it is no longer tenable. Apparent directed movement can be generated through local motor adjustments, temporal comparisons, and orienting mechanisms, and phototactic systems are widespread and mechanistically diverse, extending even to unicellular organisms (Jékely, 2009). Accordingly, the aim of the present study is not merely to show that taxis is not simple. Rather, we ask how a phototactic response that is normally adaptive and nutritionally beneficial is modulated by the animal's history of light exposure.

Acoelomorphs occupy an informative position for studying the plasticity of taxis. The clade was delineated relatively recently (Baguñà & Riutort, 2004). There is still no consensus on its exact phylogenetic placement: hypotheses variously place it as the sister group to Ambulacraria (Philippe et al., 2011, 2019) or as the basal branch of all other bilaterians (Álvarez-Presas et al., 2024; Cannon et al., 2016; Hejnol et al., 2009; Ryan et al., 2013). Either way, the group is a useful target for probing the early evolution of behavior in Bilateria. Its vermiform body plan is clearly distinct from the radial symmetry of cnidarians such as jellyfish and sea anemones, exhibiting a definite bilateral organization (Figure 1a); it also differs from the pentaradial symmetry of echinoderms (e.g., starfish), which may be close relatives. At the same time, acoelomorphs possess relatively simple nervous systems: depending on the species, neural centralization can be weak, approaching a nerve-net–like organization, whereas other species show aggregation of neurons toward the head region (Gavilán et al., 2016; Perea-Atienza et al., 2015; Sakagami et al., 2024).

Flexible behavioral adjustment has begun to be documented even in acoelomorphs. The convolutid *Praesagittifera naikaiensis* possesses small rhabdomeric eyes and exhibits positive phototaxis in response to light (Yamasu, 1991). Because it acquires nutrients via photosynthesis performed by symbiotic algae, this behavior serves a foraging function. Matsui and Hata (2025b) presented *P. naikaiensis* with a "choice" in a T-maze in which illumination differed between the two arms. As in vertebrates and arthropods, choice proportions tracked the difference in "reward" magnitude, operationalized as light intensity. This matching behavior was disrupted when animals were pre-exposed to light for 24 hours. This pattern may indicate that prior light exposure acted as "satiation," reducing behavioral sensitivity. Thus, their phototaxis is executed in a manner that depends on physiological state. They therefore provide informative models for probing the flexibility of behavior in early animal evolution.

In a closely related species, *Symsagittifera roscoffensis*, spontaneous avoidance of excessively intense light has been reported (Thomas et al., 2024). Because overly strong light can damage the symbiotic algae, intensity-dependent switching in phototactic behavior is likely adaptive. Within acoelomorpha, these taxa exhibit relatively pronounced anterior neural centralization (Gavilán et al., 2016; Perea-Atienza et al., 2015; Sakagami et al., 2024). However, light of excessively high intensity can itself exert immediate harmful effects on the organism. If behavior changes following sustained exposure to nutritionally beneficial light that would ordinarily elicit positive phototaxis, this would provide further evidence that individuals adjust their behavior in a history-dependent, state-dependent manner.

In this study, thus, we systematically examined how prior light exposure affects phototaxis in *P. naikaiensis*. In Experiment 1, we examined whether pre-exposure to light for 1 to 5 days attenuates phototaxis. This experiment revealed that phototaxis in *P. naikaiensis* was reduced by prolonged light exposure. However, this result was subject to a potential confound: the outcome of Experiment 1 could be attributed merely to debilitation caused by prolonged light exposure. Experiment 2 therefore served as a control, quantifying spontaneous locomotor activity after five days of light exposure. If the observed reduction in phototaxis had simply reflected light-induced impairment, non-phototactic locomotor activity should also have been reduced; however, this was not the case. Finally, in Experiment 3, we constructed a platform with continuously illuminated and shaded regions and allowed *P. naikaiensis* to move freely between them for five days; using this procedure, we tested whether the animals would come to avoid light spontaneously as a function of their cumulative exposure time. Across this series of experiments, we sought to show that phototaxis-driven

locomotion in *P. naikaiensis* is performed depending on the history of light exposure.

Experiment 1

Experiment 1 aimed to examine whether continuous light exposure affects positive phototaxis. Specifically, we predicted that prolonged exposure would attenuate phototaxis. To this end, *P. naikaiensis* individuals were placed in a linear track illuminated from one end. Prior to the experiment, the worms were continuously exposed to light for 0–5 day.

Materials and Method

Subjects and Housing

We used the acoel flatworm *Praesagittifera naikaiensis* collected from public beaches on Awaji Island, Hyōgo Prefecture, and Ushimado, Okayama Prefecture (Yamasu, 1982; Figure 1a). Collection locations were selected with reference to the publicly available map reported by Hikosaka-Katayama, et al. (2020).

Housing method followed Hikosaka (2015) and was identical to Matsui and Hata (2025); therefore, we describe here only procedures relevant to the present study, primarily light-related parameters. The animals were group housed in an acrylic aquarium (25 cm W × 20 cm D × 20 cm H) that was initially filled with seawater from the collection sites and then gradually replaced with artificial seawater (Delphis, Japan). The light cycle was maintained at 12 h light and 12 h dark. Illuminance ranged from approximately 2,000 to 10,000 lux depending on aquarium location. The aquarium was continuously aerated. No additional food was provided, and the animals were acclimated for at least 14 days before experimentation. After completion of the experiments, animals were returned to holding aquaria and maintained. To prevent reuse of experimental subjects, individuals were segregated into separate aquarium.

Apparatus

All experimental apparatus is shown in Figure 1b. Experiment 1 used a straight runway measuring 14.5 cm in length, 3.0 cm in width, and up to 1.5 cm in depth. The device was designed using computer-aided design software (Fusion 360; Autodesk, USA) and fabricated with a 3D printer (Bambu Lab A1; Bambu Lab, China). It was printed in semitransparent PETG. Because light was delivered from the side of the runway, a transmissive material was expected to enhance light attraction in the animals.

Phototaxis measurements and light pre-exposure were conducted using a standard LED light (LTC-LC08U-KN 06-0910, OHM, Japan). Illuminance was 10,000–12,000 lux, which was approximately comparable to the maximum illuminance in the housing aquaria. Behavior was recorded from above with a 4K-resolution webcam (ELP-USB4KCAM01H-H120, ELP, China). The experiment was performed in a dark room to prevent incidental illumination such as room lights and sunlight.

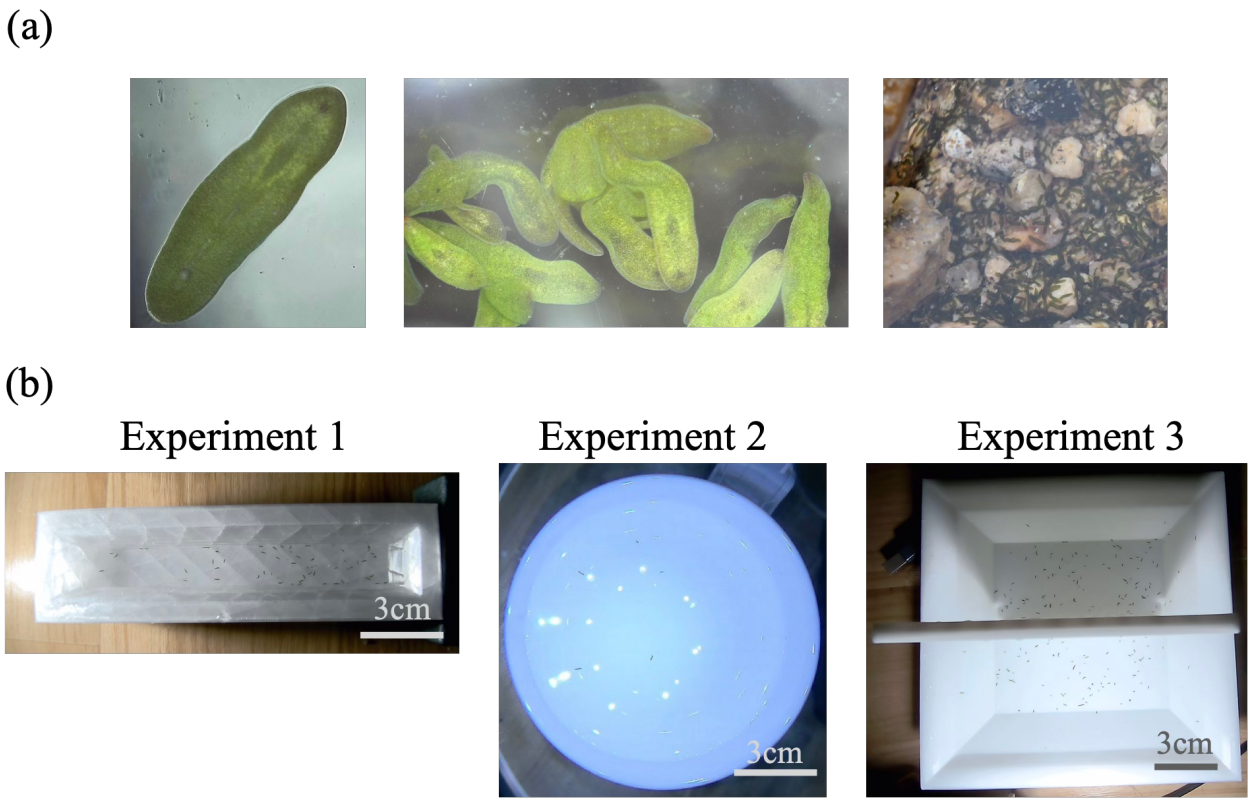
Experimental Procedure

Aggregated *P. naikaiensis* in the housing aquarium were gently aspirated with a 1 mL pipette and gently introduced to the end of the straight runway opposite the light source. The animals were then exposed to light continuously for 1 hour from the side, and their movement toward the illuminated end via phototaxis was recorded. Timing began when the last individual had been introduced into the runway. Analyses focused on the 1, 5, 15, 30, and 60 minute time points. Still images automatically captured by the camera were processed in ImageJ (National Institutes of Health, USA) to digitize individual positions and extract x and y coordinates. The number of detected individuals ranged from 40 to 94. Although sample size varied, prior work indicates that such variation does not interfere with phototaxis (Matsui & Hata, 2025b).

The animals were devided into two groups: the light pre-exposure and control groups. In the light pre-exposure group, animals were pre-exposed to light for 1 to 5 days. For this procedure, individuals were transferred to 200 mL glass cups whose tops were sealed with transparent plastic wrap to prevent evaporation. In this group, we expected phototaxis to attenuate as a function of exposure duration. In the control group, *P. naikaiensis* were housed in glass cups under the standard 12 h light and 12 h dark cycle for 1 to 5 days. To eliminate prior runway experience as a potential confounding, we used separate cohorts for each exposure duration (1 to 5 days) and did not reuse individuals across conditions.

Figure 1

Studied Species Praesagittifera naikaiensis and Experimental Apparatus



Note. (a) The right-side photo shows individuals of P. naikaiensis discovered in the tide pool at the collection site. (b) Experimental apparatus. Ellipse-like dots represent each P. naikaiensis individual.

Analysis

A three-factor analysis of variance (ANOVA) was used with all factors between subjects. The factors were condition (control or light pre-exposure), elapsed time (1, 5, 15, 30, and 60 minutes), and exposure duration (1 to 5 days). Although elapsed time would ordinarily be treated as a within-subject factor, individual identification and continuous tracking were not feasible with the present procedure, so it was analyzed as a between-subjects factor. For follow-up comparisons, we conducted pairwise *t* tests with *p* values adjusted by Holm's method. All statistical analyses and data visualizations were conducted in R (version 4.1.0).

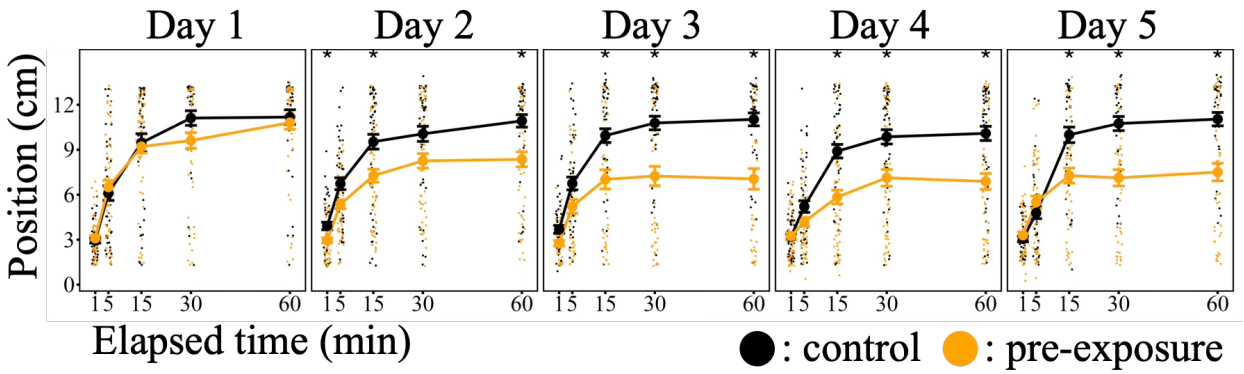
Result: The Prior Light Exposure Attenuates Phototaxis

At 60 minutes, most individuals in the control group without pre-exposure moved toward the light source (Figure 2). The ANOVA revealed that all two-way interactions were significant, including condition × elapsed time ($F(4, 2{,}444) = 17.20$, $p < .001$), condition × day ($F(4, 2{,}444) = 8.53$, $p < .001$), and elapsed time × day ($F(4, 2{,}444) = 2.00$, $p = .01$), whereas the three-way interaction (condition × elapsed time × day) was not significant ($F(16, 2{,}444) = 1.39$, $p = .13$). Accordingly, we tested differences among conditions at each elapsed-time point and within each day.

As a result, animals in the light pre-exposure group moved toward the light at approximately the same rate as controls on Day 1, and the final mean position did not differ. By Day 2, however, phototaxis in the light pre-exposure group was attenuated, and from Day 3 onward this attenuation stabilized (p values ranged from .00007 to .02). The final mean position in the control group ranged from 10.10 to 11.18 cm, whereas in the light pre-exposure group from Day 3 onward it ranged from 6.89 to 7.51 cm. Given that *P. naikaiensis* has a body length of approximately 1 to 3 mm, a 3 to 4 cm reduction in displacement represents a change of more than ten body lengths. Taken together, these results indicate that light pre-exposure gradually weakens phototaxis, reaching a plateau by Day 3.

Figure 2

Time Course of Phototaxis on a Straight Runway.



Note. The origin of the y-axis represents the end opposite to the light source. Asterisks indicate time points at which ANOVA revealed a significant difference among groups. Small dots indicate individual data points, and large dots indicate the mean (± SEM). The groups shown in each panel were tested using separate cohorts of individuals. Within each panel, the same cohort of individuals was used across conditions. However, because individual movements could not be tracked, it was not possible to determine which dots corresponded to the same individual across time points.

These results suggest that prior illumination reduced group-level phototactic displacement. As noted, *S. roscoffensis* shows an avoidance response to excessively strong light (Thomas et al., 2024). What differs from their study is that the light intensities we used are ordinarily favorable stimuli that elicit positive phototaxis. At these intensities, nutrition via photosynthesis by the algal symbionts is arguably possible, so the illuminated region is, in effect, a foraging target for *P. naikaiensis*. That prolonged light exposure attenuates phototaxis may indicate suppression of the behavior because light is no longer necessary for the animal. In other words, it may point to an interaction between metabolic processes associated with products generated by the symbionts upon light reception and the sensorimotor system comprising the neural pathway from the eyespots to the ciliary motor system. However, how these sensorimotor and metabolic systems are implemented in acoelomorpha remains unclear. We discuss this point in greater detail in the General Discussion.

The distribution of individual positions was broad at all time points, indicating that the behavior of any single individual could not be predicted reliably from the experimental condition alone. Thus, the present analysis should not be interpreted as explaining individual trajectories. Rather, it shows that prior light exposure shifted the group-level distribution of positions along the runway and reduced the average displacement toward the light source.

A potential limitation of the present experiment is that reduced phototaxis under the light pre-exposure manipulation cannot rule out debilitation caused by prolonged illumination. That is, photosynthesis produces not only nutrients but also harmful byproducts such as reactive oxygen species (Roach et al., 2015). Such byproducts might cause bodily damage and reduce motor capacity, rather than specifically altering phototaxis. Experiment 2 therefore tested this possibility by examining whether light pre-exposure affected spontaneous locomotion.

Experiment 2

Experiment 2 was designed as a follow-up to Experiment 1. The observed attenuation of phototaxis could reflect an alternative explanation: prolonged light exposure may have been harmful to *P. naikaiensis*, impairing locomotor ability rather than specifically reducing phototaxis. To rule out this possibility, we examined whether five days of light exposure reduced undirected locomotion, rather than phototaxis per se. To this end, we conducted an analogue of the open-field test, in which *P. naikaiensis* individuals were placed in a round dish under homogeneous illumination.

Materials and Method

Subjects and Housing

Collection and housing conditions for *P. naikaiensis* were identical to those in Experiment 1.

Apparatus

We used a commercially available round, flat-bottom dish (Figure 1b, center; Seria, Japan) The dish was circular (11.5 cm in diameter) and filled with seawater, allowing *P. naikaiensis* to move freely. A 4K-resolution webcam (ELP-USB4KCAM01H-H120; ELP, China) was mounted above the dish to record the horizontal movements of *P. naikaiensis*. Video was recorded at 3 Hz.

Experimental Procedure

Using the same procedure as in Experiment 1, we prepared two groups: a light pre-exposure group pre-exposed to continuous light for 5 days and a control group maintained on the standard light–dark cycle for the same duration. We included only the 5 day condition because it provided the most stringent test: if locomotion did not differ from controls after the longest exposure, shorter exposure durations would be unlikely to yield detectable impairment.

To quantify spontaneous locomotion, we used an analogue of the open-field test commonly employed in mammals. *P. naikaiensis* were gently placed in a round dish filled with seawater. Five individuals were introduced simultaneously, and three independent cohorts were tested per condition (total n = 15 per condition). Illumination was provided from above using a stand loupe light (B09FSX3Y3S; OTraki, China) arranged to minimize spatial bias.

Analysis

Locomotion was quantified using UMATracker (Yamanaka & Takeuchi, 2018; see Figure 3a for example trajectories). Identity swaps were manually detected and corrected. From the x- and y-coordinate trajectories, we computed the total distance traveled. If prolonged light exposure debilitates the animals, spontaneous locomotion should decrease. We therefore compared the total distance traveled between the control and light-exposed groups using an independent-samples *t* test.

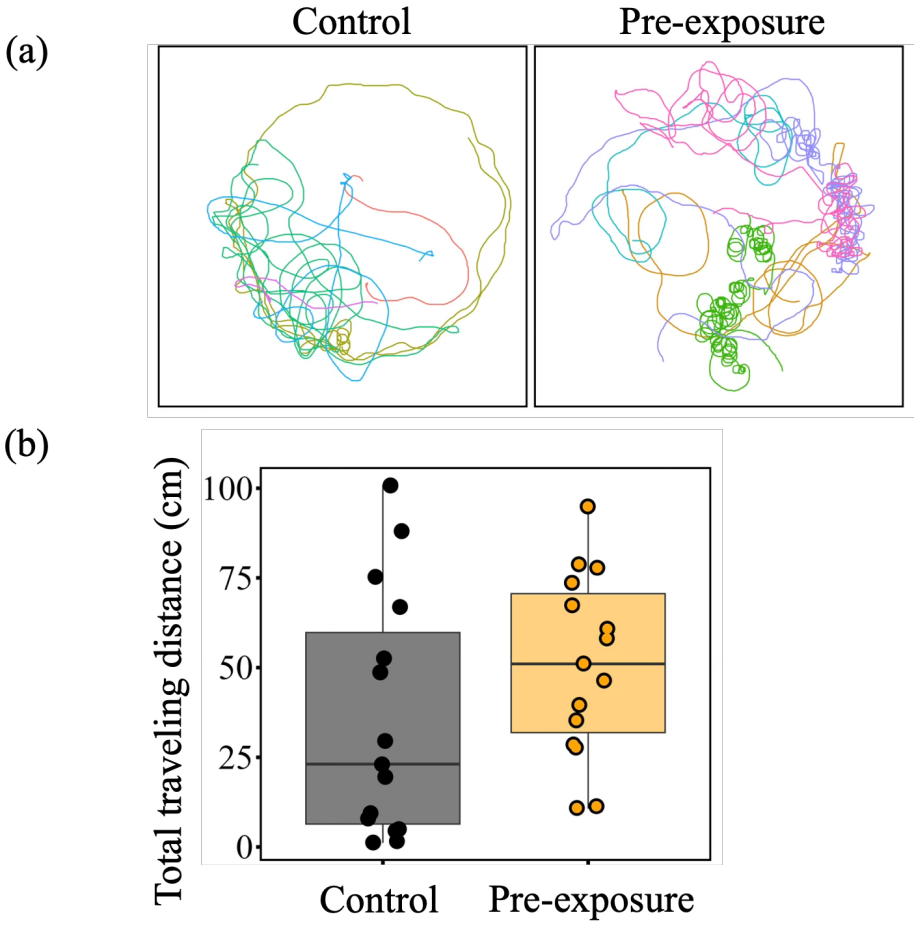
Result: Pre-exposure Did Not Detectably Reduce Gross Spontaneous Locomotion

It was visually confirmed that none of the individuals introduced into the apparatus were dead. If the reduction in phototaxis was caused by debilitation resulting from prolonged light exposure, spontaneous movement would also be expected to decrease.

Nevertheless, no significant effect of the light pre-exposure manipulation on 10-minute distance traveled was observed, $t(25.89) = 1.39$, $p = .18$. Thus, 5 days of light pre-exposure did not substantially alter spontaneous locomotion. Interindividual variability was large, with total distance ranging from near immobility to nearly 100 cm. Such long-distance movements were observed in both groups, suggesting that prolonged light exposure did not affect locomotor ability.

Figure 3

Example of Movement Trajectories of the Animals



Note. (a) Each color represents an individual. (b) Comparison of total travel distance over 10 minutes.

The observed locomotion was perhaps not based on taxis. In this setup, illumination was applied as uniformly as possible from above, and seawater salinity was kept constant, making chemotaxis unlikely. Although *P. naikaiensis* is known to exhibit positive geotaxis (Sakagami et al., 2021), geotactic behavior was unlikely to be predominant in our setup because the dish was positioned as horizontally as possible. No external stimuli were provided except for the transfer of individuals into the dish by the experimenter.

However, the following point should be noted. The present experiment does not establish that the animals' physiological state remained unchanged after light exposure. Rather, it indicates only that the reduction in phototactic displacement observed in Experiment 1 cannot be explained by a gross loss of locomotor capacity.

Taken together, across the first two experiments, we found that phototaxis is attenuated by light pre-exposure, and that this attenuation is not attributable to debilitation from excessive illumination.

Experiment 3

Prolonged illumination in *P. naikaiensis* may not only induce nutritional satiation but also be harmful, because the accumulation of toxic byproducts may damage both the symbiotic algae and the host *P. naikaiensis*. In Experiment 1, there was no shaded region, so the animals had no opportunity to avoid light. In Experiment 3, therefore, we used a platform with illuminated and shaded regions and continuously illuminated *P. naikaiensis* for five days. This setup allowed us to assess whether *P. naikaiensis* spontaneously withdraw from light depending on the duration of light they had received.

Materials and Method

Subjects and Housing

Collection and housing conditions for *P. naikaiensis* were identical to those in previous experiments.

Apparatus

The platform was shaped as an inverted square frustum with sloped sides (Figure 1b, right). Its maximum width was 15 cm, the bottom measured 9 cm, and the maximum depth was 3 cm. A central light-attenuating wall (5 mm thick) was installed to create illuminated and shaded regions. Because complete darkness would have made it difficult to count *P. naikaiensis* in the shaded region, the wall thickness was selected to attenuate, but not completely block, light. Openings on both sides of the wall allowed *P. naikaiensis* to move between the two regions (up to 3 cm wide at the top and 5 mm at the bottom). Light intensity was 10,000–12,000 lux in the illuminated region, whereas the shaded region measured 100–300 lux.

Experimental Procedure

We tested whether *P. naikaiensis* would withdraw from light over time under continuous light exposure. It was predicted that the animals would initially move toward the illuminated side due to positive phototaxis. Prolonged exposure, however, was expected to promote light avoidance as a protective response to excessive photosynthesis.

We conducted two independent 5-day experimental runs. Using a 1 mL pipette, approximately 200 *P. naikaiensis* were gently introduced onto the platform and distributed as evenly as possible between the illuminated and shaded regions. Timing began when the last individual had entered the platform. Still images were automatically captured from the overhead webcam (ELP-USB4KCAM01H-H120; ELP, China) every 10 minutes to record the positions of *P. naikaiensis*. Salinity within the platform was maintained at 30–35‰, with measurements taken approximately every 24 hours. When salinity needed to be lowered due to evaporation, roughly half of the seawater on the platform was removed with a manual pump and replaced with fresh seawater. To avoid altering the lighting geometry, the platform itself was not moved during this procedure. We continuously monitored the water removal to ensure that *P. naikaiensis* were not drawn into the pump.

The decision to introduce a large number of animals at once was based on the results of Experiment 1. In Experiment 1, the effect of light pre-exposure was evident at the level of the overall distribution, but individual animals, represented by the small dots in Figure 2, did not necessarily show the expected behavior. This suggests that the effect of prolonged exposure is detectable primarily at the group level. At the same time, however, introducing many individuals makes it almost impossible to track each animal separately. The constraints imposed by this trade-off will be addressed again as a limitation in the General Discussion.

Analysis

Unlike Experiment 1, the number of individuals in Experiment 3 was large, making manual detection impractical, so we performed automated position detection from the images at each time point. First, to generate masks delineating the illuminated and shaded regions of the platform, we applied Gaussian smoothing ($\sigma = 1.2$) to create a background image and then performed Otsu thresholding to extract the bright region. We retained only connected components with an area $\geq 15{,}000$ px² to define the platform mask and removed small holes by morphological closing. Using this mask, we classified each *P. naikaiensis* position as either illuminated or shaded. Individuals were detected with the particle-detection algorithm implemented in OpenCV's SimpleBlobDetector(). Image analysis for Experiment 3 was performed in Python (version 3.9.15).

At each 10-minute time point, we computed the occupancy probability of the illuminated region for *P. naikaiensis*. We then tested whether occupancy deviated significantly from chance using exact binomial tests. Because recordings were made every 10 minutes over 5 days (720 time points), the familywise Type I error rate was controlled using Holm's method.

Result: *P. naikaiensis* Withdrew From the Illuminated Side After 24 h of Light Exposure

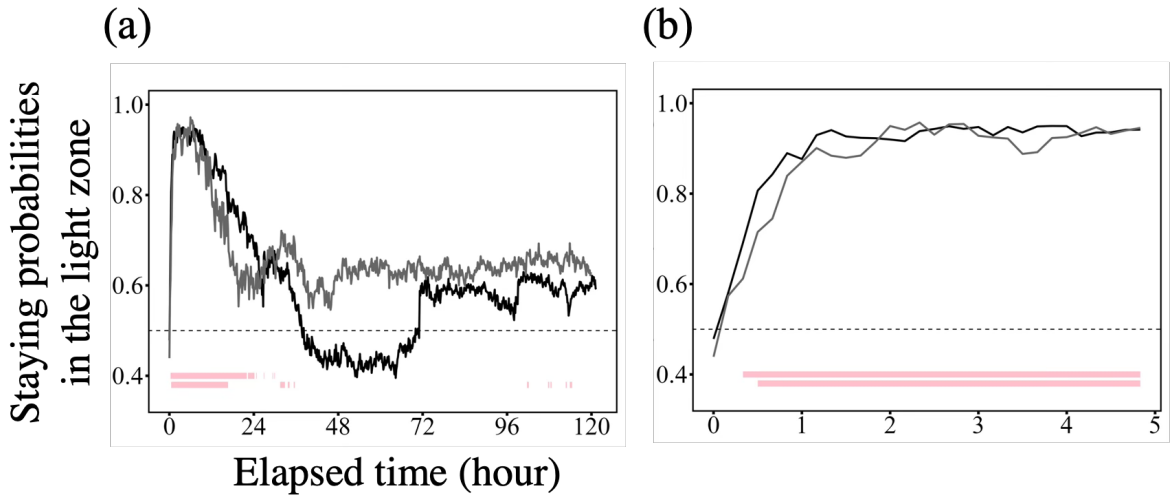
At the population level, *P. naikaiensis* did not remain on the illuminated side (Figure 4a). Animals that were initially distributed approximately evenly between the illuminated and shaded regions moved predominantly into the illuminated region within the first hour (Figure 4b), consistent with the positive phototaxis observed in Experiment 1. By around 24 h, occupancy of the illuminated region decreased: among the individuals that had been in the illuminated region (roughly 90%), approximately 30% shifted to the shaded region.

Was the 2–5 day trajectory of occupancy in the illuminated and shaded regions driven by the same individuals remaining stationary? Because measurements were taken every 10 minutes, precise individual tracking was not possible in this experiment. However, video inspection confirmed that *P. naikaiensis* occasionally engaged in spontaneous movements (https://osf.io/b6pjy/overview). Therefore, it is more likely that the observed occupancy patterns reflect active repositioning in accordance with the history of sustained illumination rather than the same individuals remaining in place.

Although relatively few time points after 24 h showed occupancy rates significantly above 50%, overall more individuals remained in the illuminated region. Occupancy of the illuminated region remained between 40% and 60% across 4 days. The fact that the mean level tended to be slightly above 50% suggests that individuals continued to prefer the illuminated region, while different individuals intermittently moved into the shaded region. Because occupancy probabilities never fell significantly below 50%, the animals did not exhibit a synchronous shift to light avoidance at the population level. This pattern suggests substantial inter-individual variation in when withdrawal from light begins as physiological state changes.

Figure 4

Probability that P. naikaiensis Individuals Occupy the Illuminated Region



Note. (a) Variation over 5 days in the probability that P. naikaiensis individuals occupy the illuminated region. (b) Close-up of the first 5 hours on Day 1.

Abrupt changes likely reflected animals being displaced by the pump stream during water exchanges. The black and gray lines indicate datasets collected on different days. Pink horizontal lines at the bottom mark the time points at which occupancy significantly deviated from 50% for the first and second datasets, respectively.

The observed behavior supports the view that the phototaxis of *P. naikaiensis* can be modulated by prior experience with light exposure. Specifically, they can change their default behavioral mode of positive phototaxis. Instead, they moved away from the illuminated side. The possible adaptive significance of this flexibility is discussed in the following section.

A limitation of Experiment 3 concerns the temporal resolution. Positions were sampled at 10-min intervals, and individual identities were not tracked continuously. Therefore, we cannot determine whether the later occupancy pattern resulted from active avoidance, reduced attraction, intermittent relocation, or other processes. The present study demonstrates modulation of group-level phototactic bias and occupancy, but it does not yet reveal the movement rules or individual decision processes that generate these patterns.

General Discussion

In contemporary animal behavior research, it is widely accepted that taxis is not as simple or automatic as it may appear. Rather, studies across multiple taxa have shown that such behavior can be history-dependent. The novel contribution of the present study lies in examining whether phototaxis in *P. naikaiensis*, a species of Acoelomorpha occupying a distinctive phylogenetic position, is modulated by the animal's history of light exposure. In *P. naikaiensis*, which derives nutrition from photosynthesis by symbiotic algae, phototaxis functions as a foraging behavior. Across three experiments, we evaluated experience-dependent modification of phototaxis in *P. naikaiensis*. Phototaxis was attenuated by prior light exposure. Moreover, when a shaded option was available, the animals inhibited positive phototaxis and spontaneously withdrew from the illuminated region.

Because history-dependent taxis has been demonstrated in several taxa, we should emphasize the significance of finding this phenomenon in acoelomorpha (Gorostiza et al., 2016; Prados et al., 2020; Thomas et al., 2024). The present study is novel in two main respects.

First, this taxon is not merely one that has been overlooked in comparative psychology: acoelomorpha may occupy a basal position within Bilateria (Álvarez-Presas et al., 2024; Cannon et al., 2016; Hejnol et al., 2009; Ryan et al., 2013). For this reason, understanding what kinds of behavior are possible in acoelomorpha may be crucial for clarifying forms of flexible behavioral control shared between vertebrate and invertebrate animals. Additionally, in terms of nervous-system organization, acoelomorpha are also characterized by weak neural centralization, placing them in a useful comparative position for examining the behavioral significance of the emergence of a well-developed central nervous system, namely, a brain (Gavilán et al., 2016; Perea-Atienza et al., 2015; Sakagami et al., 2024).

Furthermore, Invertebrate research tends to concentrate on arthropods (Collins et al., 2023; Rádai et al., 2022), and comparative psychology likewise highlights insects, arachnids, and crustaceans as major taxa (Mather, 2024). Broadening the taxonomic scope is therefore meanigful in itself. In particular, including groups with nervous systems that are expected to be close to the ancestral condition is essential for clarifying the evolutionary origins of flexible behavior. Notably, the present results suggest that state-dependent behavioral modulation was already present at an early stage of bilaterian evolution.

Second, it documents a change in responsiveness to a stimulus that is normally nutritionally beneficial. Although Thomas et al. (2024) have already demonstrated change of phototaxis in an acoelomorph species, *S. roscoffensis*, the manipulated stimulus parameter in their study was light intensity. Excessively intense light can be harmful in its own right, whereas the light used in our study was of an intensity that typically elicits positive phototaxis. It is therefore arguably a nutritionally beneficial stimulus. This is not, we believe, a trivial difference. Our results show that *P. naikaiensis* can withdraw, in a state-dependent manner, from a stimulus that would ordinarily be beneficial. This finding appears to capture a basic form of the process by which animals behaviorally adapt to shifts in physiological state, such that the stimuli they should seek change over time, as observed in vertebrates' homeostatic control.

Our results are consistent with Matsui and Hata (2025b), which suggested an interaction between the metabolic system and the sensorimotor circuitry that controls phototaxis. In that study, animals were presented with a two-arm choice, and choice proportions matched light intensity; however, after 24 hours of prior illumination, choices became more at random. In the present work, changes in responsiveness to light appeared by 48 hours in experiment 1 and by 24 hours in experiment 3. Although the procedures and apparatus differed, both sets of findings demonstrate plasticity in behavior that appears reflexive at first glance. In acoelomorphs, the symbiotic algae in *P. naikaiensis* are not intracellular but are embedded in the intercellular spaces of subepidermal tissues (Arboleda et al., 2018; Bailly et al., 2014). The route by which amino acids and other products generated by photosynthesis enter the body remains unresolved, but it is likely that metabolic processes modulate the sensorimotor system that produces phototaxis.

Why would an animal that derives nutrition from photosynthesis by its symbiotic algae need to withdrew from light? A plausible reason is that receiving excessive amount of light is likely harmful to the symbionts (Barber & Andersson, 1992). Prolonged high-intensity illumination induces photoinhibition, a decline in photosynthetic efficiency. This arises from toxic byproducts generated during photochemical reactions, whose removal is required for repair. Under ordinary conditions, repair mechanisms maintain algal viability; however, when strong light coincides with environmental stress, repair cannot keep pace, photosynthetic capacity is lost, and in the worst case, cells die. Accordingly, altering the sign of phototaxis in accordance with cumulative light exposure, not mere attenuation of it, appears adaptive for safeguarding both the animal and its symbiotic algae.

A limitation of the present study is that the light pre-exposure manipulation may have altered multiple physiological processes simultaneously. The contrast between the standard 12 h light and 12 h dark regimen and continuous illumination was designed to test whether cumulative light exposure changes phototaxis, but it cannot separate the effects of photosynthetic product availability, oxidative stress, circadian disruption, changes in symbiont condition, or other host metabolic responses. Experiment 2 shows only that five days of continuous light exposure did not produce a detectable reduction in gross locomotor capacity. It does not rule out more specific physiological changes that could bias orientation, motivation, or responsiveness to light. Therefore, the present findings should be interpreted as behavioral evidence that phototaxis is modulated by the history of light exposure, not as evidence identifying the particular metabolic mechanism responsible for that modulation.

Future work should examine the host and symbiont sides of this process more directly. For example, measurements of photosynthetic efficiency, symbiont density or condition, oxidative stress, and metabolites transferred from symbionts to the host would help determine whether withdrawal from light reflects host nutritional state, symbiont stress, or a regulatory compromise between the two. Such analyses will be necessary to understand what it means, behaviorally, for *P. naikaiensis* to be a photosymbiotic organism.

It is also necessary to acknowledge a methodological limitation of Experiment 3, which constrains the interpretation of our results. In this experiment, we found that the proportion of animals remaining on the illuminated side decreased at the group level, but individual-based tracking was technically difficult. Because the occupancy ratio differed over time, it is reasonable to infer that the animals moved between regions. Thus, the results suggest that, as a consequence of light exposure, some individuals shifted into the shaded region. However, more detailed observations at the individual level might reveal phenomena such as periodic behavioral rhythms or individual differences in orientation toward light. Our procedure may have missed these aspects, and this should be noted as an important limitation.

Finally, state-dependent adjustment of behavior, in a broad sense, has been documented across diverse taxa. In humans, hunger, an internal physiological state, modulates responses to current environmental stimuli (Loeber et al., 2013). In fishes, aggressive interactions alter hormonal dynamics and subsequently influence behavior (Earley et al., 2013). In arthropods, sawflies adjust the trade-off between food discovery and predation risk according to prior starvation experience (Singh et al., 2023). These flexible adjustments are mediated by interactions between central neural information processing and peripheral bodily states. Our study suggests that *P. naikaiensis* may possess mechanisms for monitoring its own nutritional status and the health of its algal symbionts, although how this information is conveyed to the sensorimotor system that generates phototaxis remains unknown. Given that acoelomorpha likely retain a primitive form of neural organization among bilaterians, such mechanisms may have already been present early in bilaterian evolution and could have contributed to the emergence of goal-directed behavior.

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Authorship Contribution

HM: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – review & editing, Writing – original draft. YM: Conceptualization, Methodology, Writing – review & editing. All authors reviewed the manuscript.

Data Availability

All data and codes are publicly available at https://github.com/HeathRossie/naikaiensis_phototaxis. The 3D-printable files for Experiments 1 and 3 are also available and may be modified and reused with appropriate citation (https://github.com/HeathRossie/stlfiles)

Declaration of Generative AI Usage

During the preparation of this work the authors used chatGPT 5.2 with Thinking mode in order to refine the manuscripts written by non-native English speakers. After using this tool/service, the authors reviewed and edited the content as needed and takes full responsibility for the content of the publication.

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