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Effects of UV-B radiation on fitness related behaviors of the sea urchin *Strongylocentrotus intermedius**

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Abstract Ozone depletion induced by anthropogenic gases has been increasing the transmission of solar ultraviolet-B radiation (UV-B, 280–315 nm) through the atmosphere, which may impact the fitness of marine invertebrates in intertidal and shallow waters. To our knowledge, however, the responses of fitness related behaviors to UV-B radiation at different intensities have been rarely studied in marine invertebrates. For the first time, the present study investigated the effects of exposure of one hour to UV-B radiation at different intensities on foraging behavior, Aristotle's lantern reflex and righting behavior of the sea urchin *Strongylocentrotus intermedius*. Exposure of one hour to UV-B radiation at 10 μW/cm^2 significantly reduced foraging behavior. An intensity dependent effect of exposure to UV-B radiation was found in the duration of the Aristotle's lantern reflex. Exposure to UV-B radiation at 20 μW/cm^2 for one hour significantly reduced the duration of the Aristotle's lantern reflex, but 10 μW/cm^2 did not. There was no significant difference of righting response time among sea urchins exposed to 0, 10 and 20 μW/cm^2 for one hour. To test potential carryover effects, the behavioral traits were re-measured three days later. We found significant carryover effects of UV-B radiation on foraging time and righting response time, but not on the duration of the Aristotle's lantern reflex. The present study indicates that a brief exposure of one hour to UV-B radiation can significantly affect the duration of Aristotle's lantern reflex, righting response time and foraging behavior of a sea urchin, although the immediate impacts and carryover effects were highly trait dependent. This study provides new information into the behavioral responses of marine invertebrates to exposure to UV-B radiation. Future studies should be carried out to investigate long-term carryover effects of UV-B radiation on behavioral and physiological fitness related traits.

Keyword: sea urchin; UV-B; foraging behavior; righting behavior; Aristotle's lantern reflex; fitness

1 INTRODUCTION

Ozone depletion induced by anthropogenic gases has been greatly increasing the transmission of solar ultraviolet-B radiation (UV-B, 280–315 nm) through the atmosphere (Day and Neale, 2002; Manney et al., 2011). At least ten percent of UV-B can penetrate to seawater to a depth of 16 m (Tedetti and Sempéré, 2006), highlighting the possible impacts to the fitness of marine invertebrates in intertidal and shallow water. Behaviors are an adaptive driver in evolution (Mayr, 1960; Corning, 2014). Thus, it is important to fully understand the effects of UV-B radiation on fitness related behaviors in ecologically important marine invertebrates (Lamare et al., 2011). Foraging and feeding behaviors are not only essential for the fitness of marine organisms (Grémillet et al., 2016), but important for the ecological interaction in the

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ecosystem. Righting behavior, which refers to the regaining of the normal posture after a sea urchin has been displaced, is essential for normal functioning (Brothers and McClintock, 2015). The responses of these behaviors to UV-B radiation at different intensities have not been investigated in sea urchins, despite their ecological importance.

Sea urchins are a group of ecologically important marine invertebrates in structuring marine benthic communities, both as grazers and prey (Pearse, 2006). Species inhabit intertidal and shallow waters are sensitive and susceptible to UV-B radiation in a series of biological levels, from molecular to population (reviewed by Lamare et al., 2011). Given the limited motility capability of sea urchins, behavioral responses are important to minimize potential risks of UV-B radiation. For example, covering behavior of sea urchins is significantly induced by solar radiation (Adams, 2001; Kehas et al., 2005; Sigg et al., 2007). As a representative herbivorous grazer in intertidal and shallow waters (0–13 m in depth), the sea urchin *Strongylocentrotus intermedius* has obvious foraging, Aristotle's lantern reflex and righting behaviors (Chang et al., 2004; Agatsuma, 2013). Thus, *S. intermedius* can be a good research model for the scientific question involved.

Intensity is an important concern for UV-B radiation. A global assessment of UV-B radiation shows that annual dose of UV-B radiation was ~2 to 16 MJ/(m^2·yr) at a number of observation points in the northern hemisphere (Bais et al., 2015), indicating an average intensity of ~6.3–50.4 μW/cm^2. Since *S. intermedius* inhabits waters around Japan, Korea, northeastern China and Far East Russia (Agatsuma, 2013), it is especially important to consider of the annual dose of UV-B radiation around these areas. This was ~6 MJ/(m^2·yr) (~18.9 μW/cm^2) at Tokyo (Bais et al., 2015). Although all these data of UV-B radiation were observed by land-based spectroradiometers, we would consider 10 μW/cm^2 as a reasonable intensity for laboratory simulations, because *S. intermedius* inhabits intertidal and shallow waters. Adams (2001) used the UV-B radiation at 10 μW/cm^2 to test the covering response of the sea urchin *Strongylocentrotus droebachiensis*. However, we do not know how UV-B radiation at a greater intensity (for example, 20 μW/cm^2) affects the behaviors of sea urchins, leaving the intensity effect largely untested.

The main aims of the present study are to investigate 1) the effects of UV-B radiation at different intensities on foraging, the Aristotle's lantern reflex and righting behavior of *S. intermedius*, and 2) the potential carryover effects of the UV-B radiations on these fitness related behaviors.

2 MATERIAL AND METHOD

2.1 Sea urchins

Juvenile *S. intermedius*, which were originally bred in October 2014, were transported from the hatchery of Dalian Haibao Fishery Company to the Key Laboratory of Mariculture and Stock Enhancement in North China's Sea, Ministry of Agriculture at Dalian Ocean University on March 5, 2015. The sea urchins were reared at a relatively low density of ~ 5 kg/m^3 in a large tank (length × width × height: 180 cm×100 cm×80 cm) with continuously aerated seawater until the experiment started on July 23, 2016. They were fed wild fresh *Saccharina japonica* and *Ulva lactuca ad libitum* according to availability under natural photoperiod (from 8 h light: 16 h dark to 16 h light: 8 h dark) at the laboratory. The seawater was changed every three days.

Sea urchins were not fed for three days before the experiment to standardize their condition. Test diameter, test height and body weight were measured before the experiments using a digital vernier caliper (Mahr Co., Germany) and an electric balance (G&G Co., USA).

2.2 Experimental design

Three levels of UV-B radiation were set at 0, 10 and 20 μW/cm^2 (~ 20 cm depth). Sea urchins were put in individual cages at a depth of ~20 cm for UV-B radiation. They were exposed to UV-B exposure for one hour using a UV-B lamp (TL 40 W/12 RS, Philips Co., Germany). The intensities of UV-B radiation (10 and 20 μW/cm^2) were set by regulating the distance between UV-B lamp and the surface of the water (Adams, 2001). The real intensities of the two groups were 10±1.5 μW/cm^2 and 20±2 μW/cm^2, which were measured with an underwater UV-B radiation meter (Photoelectric Instrument Company of Beijing Normal University, China). Individuals not exposed to UV-B radiation were the control (0 μW/cm^2).

Foraging time, duration of Aristotle's lantern reflex and righting response time were measured immediately after the UV-B radiation (day 0). All sea urchins were subsequently put into individual cages in a large tank (180 cm×100 cm×80 cm) after

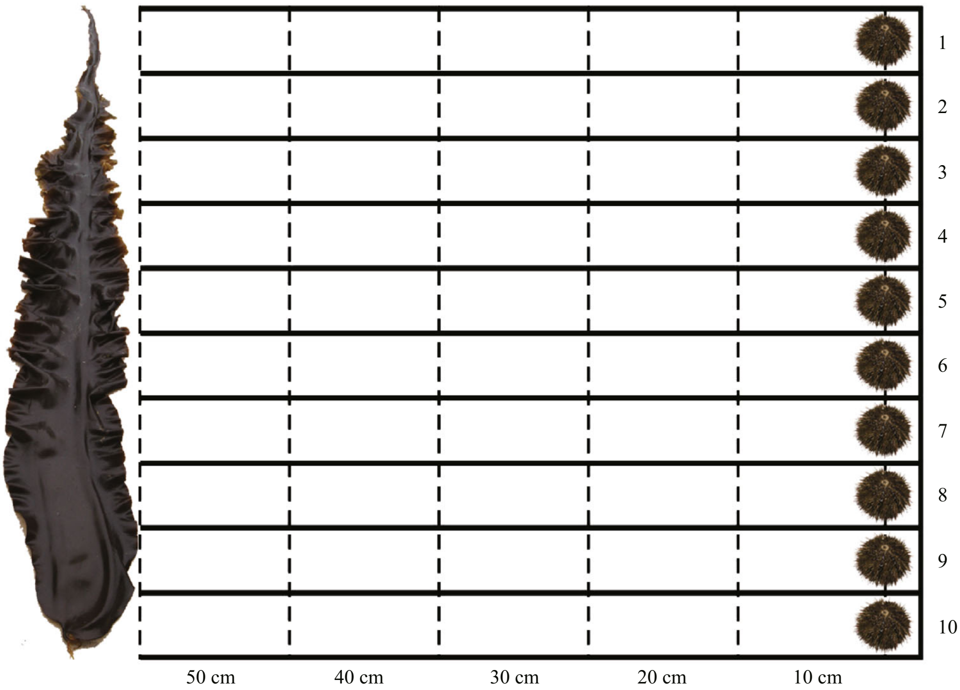

Fig.1 Diagram of the sea urchin raceway used for measuring foraging behavior of *S. intermedius*

A large piece of *S. japonica* was placed at the end of the raceway.

behavioral measurements on day 0. They were maintained in continuously aerated seawater and fed wild fresh *S. japonica ad libitum* for 3 days. To test potential carryover effects of UV-B radiations, all the behavioral traits were re-measured 3 days after radiation (day 3).

All behaviors were measured under similar illumination of ~200 lx, without UV-B radiation and under similar water quality (water temperature 21.7–22.8°C, pH: 8.09–8.27, salinity: 31.86–32.71, dissolved oxygen: 6.3–7.1 mg/L). Notably, different sea urchins were used in different behavioral experiments.

2.3 Foraging time

The measurement design of foraging behavior is mainly based on the finding of Machiguchi (1987) that *S. intermedius* were attracted to water passed over kelp eaten by sea urchins. Foraging time of *S. intermedius* were measured in sea urchin raceways using a digital video (Legria HF20, Canon), according to the method of Barry et al. (2014) with some revisions (Fig.1). It can be summarized as follows:

The device, which contains 10 separated acrylic raceways (length × width: 50 cm×6 cm), was placed in a large tank (180 cm×100 cm×80 cm) with ~1 000 L aerated still water for the measurements. Still water was used because the measurements were carried out in a relatively large tank within 30 min and then changed for the next round. The separation of raceways ensures the data independence required for statistical analysis (Barry et al., 2014). We measured foraging behavior of twenty *S. intermedius* for each group (*n*=20).

Foraging time refers to the time required for each sea urchin to move to a large piece of *S. japonica* at the end of the raceway (Fig.1, Barry et al., 2014). Foraging time was counted as 1 800 s if the individual did not reach the kelp within 30 min.

2.4 Duration of Aristotle's lantern reflex

The Aristotle's lantern reflex represents the capability of sea urchins to grasp a food item with their teeth (Brothers and McClintock, 2015). It was measured following the method of Brothers and McClintock (2015) with some revisions. We put inverted *S. intermedius* on a laboratory table for individual measurement. A kelp-based food coated steel probe (diameter=2 mm) was used to touch the mouth of *S. intermedius*. Duration of Aristotle's lantern reflex, which refers to the constant reflex duration of the response of the teeth to the steel probe, was recorded. We individually measured duration of Aristotle's lantern reflex of twenty *S. intermedius* for each group (*n*=20).

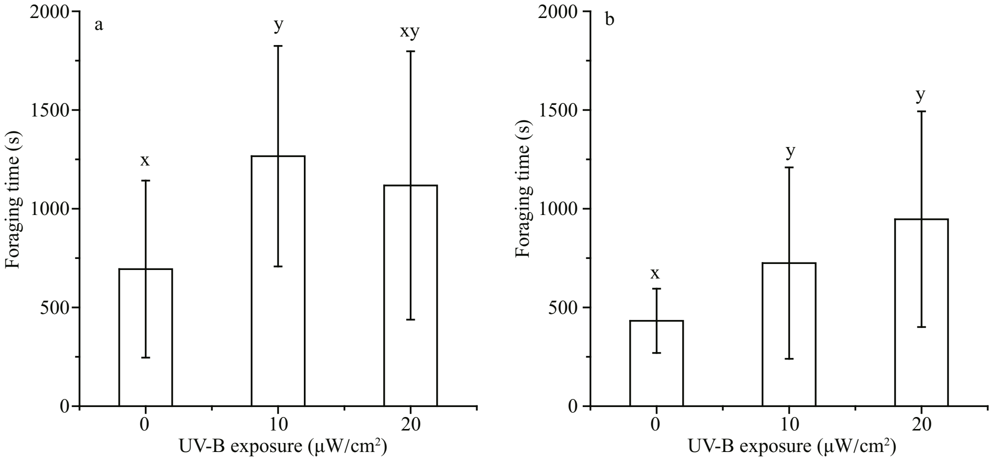

Fig.2 Foraging time of *S. intermedius* on day 0 (a) and day 3 (b) after exposure to UV-B radiation of different intensities (*n*=20, mean±SD)

Different letters above the bars refer to significant difference among experimental groups.

2.5 Righting response time

Righting response time refers to the length of time required for inverted *S. intermedius* to right themselves with the aboral side up within 10 min. It was individually measured in tanks (600 mm×350 mm×200 mm). One *S. intermedius* was gently placed on the bottom of a tank with their aboral side down. Righting response time was recorded. The relatively large tanks were used to avoid possible influence of the tank wall on righting behavior. Aeration and running seawater were not used in measurement to avoid potential impacts on righting behavior. We measured righting behavior of twenty *S. intermedius* for each group (*n*=20).

2.6 Statistical analysis

The data were tested for homogeneity of variance and normal distribution using Levene's test and Kolmogorov-Smirnov test, respectively. We used Kruskal-Wallis ANOVA followed by all pairwise multiple comparisons to analyze foraging time, righting response time and duration of Aristotle's lantern reflex, because of the non-normal distribution and/or heterogeneity of variance of the data even after data transformations. All data analysis was performed using SPSS 16.0 statistical software. A probability level of $P<0.05$ was considered as significant.

3 RESULT

3.1 Foraging time

There was no significant difference in test diameter ((38.43±2.18) mm), test height ((18.44±1.32) mm) and body weight ((21.97±3.34) g) of *S. intermedius* among experimental groups used for measuring foraging time (P=0.611, 0.318 and 0.279).

Strongylocentrotus intermedius exposed to UV-B radiation at 10 μW/cm² for one hour showed significantly longer foraging time than those not exposed to UV-B radiation (Kruskal-Wallis χ^2=-17.009, P=0.005, Fig.2a). However, foraging time of *S. intermedius* did not differ significantly between the groups of 10 and 20 μW/cm² (Kruskal-Wallis χ^2=5.342, P=0.959).

On the third day after the UV-B radiation (day 3), *S. intermedius* in the groups exposed to 10 and 20 μW/cm² for one hour consistently showed significantly longer foraging time than those not exposed to UV-B radiation (0–10 μW/cm²: Kruskal-Wallis χ^2=-13.750, P=0.038; 0–20 μW/cm²: Kruskal-Wallis χ^2=-20.150, P=0.001; Fig.2b). No significant difference of foraging time was found between the groups exposed to 10 and 20 μW/cm² (Kruskal-Wallis χ^2=-6.400, P=0.738).

3.2 Duration of Aristotle's lantern reflex

There was no significant difference in test diameter ((37.97±1.72) mm), test height ((18.22±1.30) mm) and body weight ((21.79±2.76) g) of *S. intermedius* among experimental groups for duration of Aristotle's lantern reflex (P=0.378, 0.161 and 0.179).

Strongylocentrotus intermedius exposed to UV-B radiation at 20 μW/cm² showed significantly shorter duration of Aristotle's lantern reflex than those not exposed to UV-B radiation (Kruskal-Wallis χ^2=14.000, P=0.031, Fig.3a). No significant difference was found in *S. intermedius* between the groups

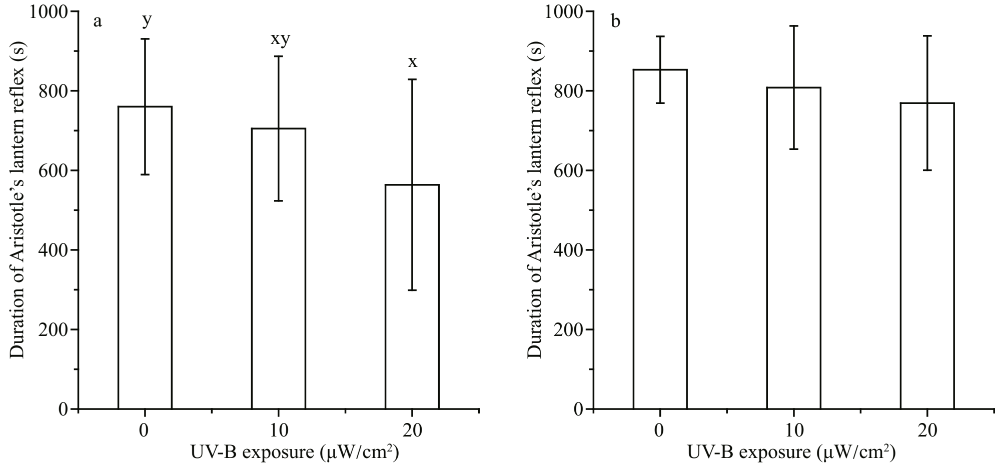

Fig.3 Duration of Aristotle's lantern reflex of *S. intermedius* on day 0 (a) and day 3 (b) after exposure to UV-B radiation of different intensities (*n*=20, mean±SD)

Different letters above the bars refer to significant difference among experimental groups.

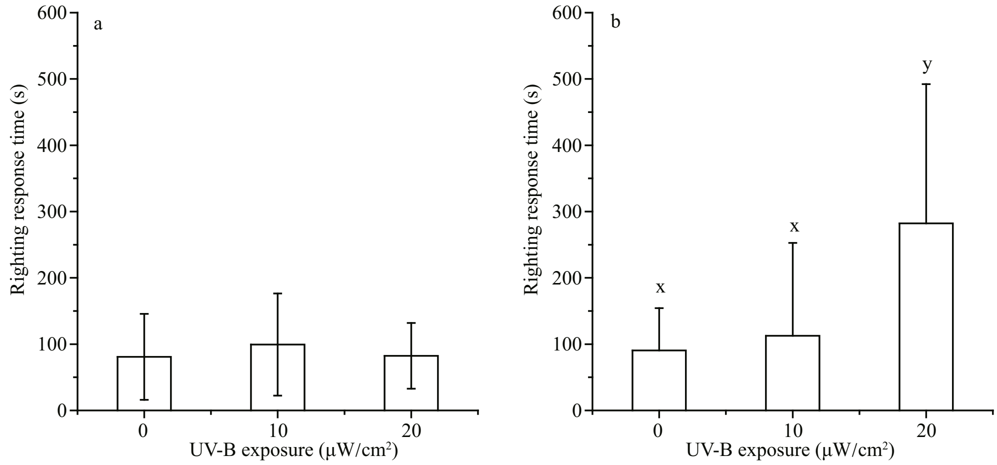

Fig.4 Righting response time of *S. intermedius* on day 0 (a) and day 3 (b) after exposure to UV-B radiation of different intensities (*n*=20, mean±SD)

Different letters above the bars refer to significant difference among experimental groups.

exposed to 10 and 20 μW/cm^2 (Kruskal-Wallis χ^2=8.275, *P*=0.386).

Three days later (day 3), however, there was no significant difference of duration of Aristotle's lantern reflex among all the three groups (Kruskal-Wallis χ^2=2.717, *P*=0.257, Fig.3b).

3.3 Righting response time

There was no significant difference in test diameter ((39.22±1.98) mm), test height ((22.10±1.83) mm) and body weight ((21.79±2.76) g) of *S. intermedius* among experimental groups for righting response time (*P*=0.293, 0.981 and 0.725).

Strongylocentrotus intermedius showed no significant difference of righting response time among the three groups (Kruskal-Wallis χ^2=0.558, *P*=0.756, Fig.4a).

Three days later (day 3), however, righting response time of *S. intermedius* exposed to 20 μW/cm^2 was significantly longer than those in the groups of 0 and 10 μW/cm^2 (0–20 μW/cm^2: Kruskal-Wallis χ^2=-18.950, *P*=0.001; 10–20 μW/cm^2: Kruskal-Wallis χ^2=-18.170, *P*=0.003, Fig.4b). There was no significant difference between latter two groups (Kruskal-Wallis χ^2=-0.780, *P*=1.000).

4 DISCUSSION

Ultraviolet radiation induces significant negative phototaxis (for example, sheltering behavior) and covering behavior of sea urchins (Adams, 2001;

Verling et al., 2002; Dumont et al., 2007; Sigg et al., 2007). These behaviors are potentially important to their fitness (Zhao et al., 2016). However, sea urchins do not necessarily hide themselves for long periods because they need to forage and feed after strong ultraviolet radiation. For the first time, the present study investigated the effects of one hour exposure to UV-B radiation at different intensities on several fitness related behaviors of sea urchins: foraging behavior, Aristotle's lantern reflex and righting behavior. Further, to test the possibility of carryover effects, these behavioral traits were re-measured three days later. This study provides new information into behavioral responses of marine invertebrates to exposure to UV-B radiation.

Foraging behavior has been well studied in sea urchins, not only due to the importance for their own fitness, but because heavy foraging pressure has major effects on coastal algal communities (Agatsuma et al., 2000; Miyamoto and Kohshima, 2006; Barry et al., 2014; Harding and Scheibling, 2015). In the present study, we found that foraging behavior was significantly reduced in *S. intermedius* exposed to UV-B radiation at 10 μW/cm^2 for one hour compared to those not exposed to UV-B radiation. This result partially agrees with the finding of Barry et al. (2014) that foraging time was significantly longer in the sea urchin *Strongylocentrotus fragilis* exposed to ocean acidification (pH ~7.14; pCO_2 ~3 255×10^{-6}). The present result clearly indicates that short-term (one hour) UV-B radiation can significantly impact foraging behavior of sea urchins. Further, carryover effects on foraging time were consistently found in *S. intermedius* three days after the one hour exposure to UV-B radiation at both 10 and 20 μW/cm^2. This suggests that the reduced foraging behavior of *S. intermedius* would last at least three days after exposure to UV-B radiation, which potentially triggers a serious decreasing of the fitness of sea urchins.

Aristotle's lantern reflex, which demonstrates the capability of sea urchins to manipulate their jaws to grasp food, is another important concern for the feeding efficiency of sea urchins (Brothers and McClintock, 2015). In the present study, *S. intermedius* exposed to UV-B radiation at 20 μW/cm^2 (but not 10 μW/cm^2) showed significantly shorter duration of Aristotle's lantern reflex than those not exposed to UV-B radiation, suggesting that the capability of Aristotle's lantern reflex of sea urchins exposed to UV-B radiation is intensity dependent. This result is consistent with Brothers and McClintock (2015) that sea urchins *Lytechinus variegatus* exposed to 32°C had significantly fewer lantern reflexes than those exposed to 28°C. When feeding, the teeth of Aristotle's lantern are manipulated by retractor, comminatory, protractor, and postural muscles to grasp and masticate food (De Ridder and Lawrence, 1982). Thus, the significantly reduced duration of Aristotle's lantern reflex indicates that feeding efficiency can be greatly impacted and fitness consequently decease. Unexpectedly, however, there was no significant difference on duration of Aristotle's lantern reflex among all groups three days after UV-B radiation. This result indicates that Aristotle's lantern reflex can be recovered from exposure to 20 μW/cm^2 UV-B after three days. This means that Aristotle's lantern reflex is more resilient than foraging behavior, probably because of the well known phenotypic plasticity of Aristotle's lantern of sea urchins (Ebert et al., 2014).

Righting behavior is essential for sea urchins to escape from predatory and physical turbulence (Brothers and McClintock, 2015) and consequently is important for their fitness. In the present study, exposure for one hour to UV-B radiation at both 10 and 20 μW/cm^2 did not significantly affect righting response time of *S. intermedius*. This indicates that righting behavior is relatively robust even in the exposure of UV-B. However, *S. intermedius* exposed to UV-B radiation at 20 μW/cm^2 showed significant carryover effect on righting response time three days later. This indicates a delayed effect instead of an immediate response. It partially agrees to the finding of Brothers and McClintock (2015) that chronic elevation of seawater temperature (for 10 days) significantly reduced righting behavior of *L. variegatus* compared to an acute elevation (for 1 days).

5 CONCLUSION

Exposure to UV-B radiations at 10 μW/cm^2 for one hour significantly reduced foraging behavior of *S. intermedius*. An intensity dependent effect of exposure to UV-B radiation was found for the Aristotle's lantern reflex time of *S. intermedius*, in which exposure to 20 μW/cm^2 of UV-B radiation significantly reduced duration of Aristotle's lantern reflex, but 10 μW/cm^2 did not. There was no significant difference of righting response time among all experimental groups. There were significant carryover effects of exposure to UV-B radiation on foraging time and righting response time, but not on duration of Aristotle's lantern reflex.

6 DATA AVAILABILITY STATEMENT

The datasets during and/or analyzed during the current study are available from the corresponding author upon request.

7 ACKNOWLEDGMENT

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